PHYTOPATHOLOGY

VOLUME XV NUMBER 9

SEPTEMBER, 1925

THE PROBLEM OF HOST SELECTION AND HOST SPECIALIZATION OF CERTAIN PLANT-INFESTING NEMAS AND ITS APPLICATION IN THE STUDY OF NEMIC PESTS[1]

G. STEINER

WITH EIGHT FIGURES IN THE TEXT

INTRODUCTION

One of the most fascinating chapters in the study of plant-parasitic nemas is that dealing with their ability to find and select the proper host plant. The whole complex of known facts and still open questions centering about this mutual relationship of plants and nemas is perhaps best designated as the problem of host selection. Although not so recognized, this problem has played an exceedingly important role both during the past and present in the many attempts towards an applicable control of nemic plant-pests. To prove this we need only to recall the catch- or trap-plant method of Kühn (28), the recently outlined "Reizpflanzen methode" of Baunacke (3), the crop-rotation methods, the method of activation of the cysts of the sugar beet nema by Rensch (45), etc. These are all based or built up on the known facts of the stimulative influence of the host plant upon the parasite. During the last twenty or thirty years much work has been expended on the study of the so-called susceptibility and resistance of certain plants, or plant varieties, to nemic pests with a view of the possible breeding of immune or resistant crops. All the endeavor along these lines did not lead to any notable result, because of the complete ignoring of the host-selection problem, which here is of fundamental importance. Most of the investigators noted the peculiar behavior of the pest-producing nemas in selecting their plant hosts, but unfortunately did not recognize the primary importance of these facts.

[1] The writer is indebted to Dr. Hall, of the Bureau of Animal Industry, for some literature; to Dr. Godfrey, Mr. Leukel, and Mr. Thorne, of the Bureau of Plant Industry, for some nema material, and to Dr. Arzberger, also of this Bureau, for the unpublished results of his investigations on the morphology of the roots of so-called nema-resistant cowpea varieties. Dr. Cobb kindly revised the manuscript and made some helpful suggestions.

Besides these more practical questions, our host selection problem involves a series of important and interesting theoretical aspects: questions of physiology, morphology, genetics, soil chemistry, soil physics, etc., etc., are connected with it.

It is the aim of the present paper to outline the problem, to analyze its present state, to describe the whole host-selection mechanism combined with existing host specialization as seen in the light of our present knowledge, and to show its importance and application. The writer is convinced that his conception not only explains many facts brought up by the earlier and present investigators as inexplicable and contradictory, but also makes it possible to work out more effective methods for the control of nemic pests, as, for example, scientific crop-rotation methods. Furthermore it will give the breeders and searchers for resistant or immune varieties a sound basis for their experiments and will open many lines of further attack of the whole problem of nemic plant-pests.

GENERAL PART

The Behavior of Plant-Infesting Nemas in Selecting Their Hosts

Soil is the life medium of the nemas to be considered here, a medium which, compared with water and air, isolates its inhabitants to a high degree. Soil is not transparent and it opposes the greatest obstacles to any movement, and seems, therefore, to separate and isolate the members of its life association in a most pronounced way. Yet the soil nemas are perfectly able to orient themselves in this medium, and locate their food and also their mating partners, even at considerable distances.

Our chief species of plant-infesting nemas attack a large number of different plant species, which are called their hosts. But there are hosts of different degrees. By this it is not to be understood that some species are, in general, more preferred than others. Different populations of the same nema species may behave quite differently toward one host plant, that is, one population will attack it heavily, and another not at all. The different populations of a nema species may each have a different preferred host plant. If a number of different host plants are growing on a given soil area, the nemas in the soil will always find out and attack the one they like best, leaving the others unharmed, even though they too are favored host plants of that species of nemas. How they are capable of doing this is a problem of much interest and importance, and will be explained later, according to our present knowledge.

A number of examples gathered from literature best give an idea of the strange and peculiar behavior the nemas very often show in selecting their host plants. Heretofore no explanation was given for this behavior,

although it greatly puzzled many investigators and was a source of much controversy and many mistakes.

A very significant case has been described by Liebscher (30) from the Agricultural Experiment Station at Göttingen, Germany. I tried to condense this case in the schematic figure 1. A plot of ground of the experi-

FIG. 1. Schematic representation of the experiments of Liebscher with two populations of *Heterodera schachtii*, the one highly specialized on peas, the other on oats.

ment station was, with one exception, continually planted with peas for about thirteen years; finally it became so badly infested with *Heterodera schachtii* that the harvest amounted to only 4% of the seed material. Separated from this plot of peas by a path of one meter was a plot on which, for seventeen years, oats had been planted. This plot was also highly infested with *H. schachtii* and declared to be "oatsick." Liebscher then planted on both plots (separated only by the aforementioned path of one meter in width) a number of crop-plants in order to find out how the nemas would behave toward them. The schematic figure gives the results. The *H. schachtii* populations on these two plots behaved, as can be seen, very differently toward the same series of host plants. Plants attacked by the population which had lived for years on peas were not attacked at all by that which had lived continually on oats, and vice versa. It can easily be understood that Liebscher, through these experimental results, came to the conclusion that the pea-nemas were a new form (*Heterodera goettingiana*), because they did not attack the usual host of *H. schachtii*, the sugar beet. He was apparently wrong in this conclusion, but nobody can blame him in the face of his striking results.

Today we see the situation in Liebscher's case as follows: The *Heterodera* populations on both plots were probably first identical, starting from the same infestation. Then the population on the pea plot lived for years, that is, for a long series of generations, exclusively on peas, and became highly specialized on this host. The population of the other plot, however, for at least seventeen years, i.e., for about seventy generations, lived on oats and had become highly specialized on this plant.

The relations of *H. schachtii* to oats have also been discussed by Fuchs (19, pp. 946–947) who calls attention to the fact that sometimes oats are attacked as heavily as sugar beets, while in other cases they are only slightly affected. Fuchs mentions the possibility of the segregation of races but doubts whether this would explain all the observed facts. In general he found that the *H. schachtii* specimens which he used would attack sugar beets, white mustard, and oats, with equal facility. But on one occasion he was unable to get oats infested, whereas sugar beets and white mustard, sowed three weeks later between these same oats, were heavily attacked. Why this varying behavior? Apparently the last population of *H. schachtii* Fuchs worked with was, in a very pronounced way, specialized on sugar beets and their nearest related plant species.

Some investigators class the members of the Solanaceae as being nonsusceptible to *H. schachtii* (Hollrung (25) and Kühn (28) used potatoes as crop following catch-plant sowings), while later, various authors found that potatoes were heavily attacked and that some weeds from the Solanaceae family were the most important propagators (3, 65). These contra-

dictory statements can easily be understood. The *H. schachtii* populations with which these different investigators worked were specialized along different host lines. For the same nema species, the chicory was hitherto regarded as one of the most pronounced non-susceptible plants, and yet Baunacke (3, p. 211) quotes G. Plümecke who found this very plant also attacked by *H. schachtii*. It seems quite as if a much larger number of plants than hitherto thought could be hosts of this nema if the latter has sufficient time to adapt itself to it.

In quite recent years a similar case of a population of *H. schachtii*, specialized to such a degree on peas that sugar beets were hardly affected by them, was recorded by M. Capus (10) from the Gironde in France. In connection with the statement, that, in the experiments of Kühn, the *H. schachtii* from sugar beets did not attack peas, Hollrung (24) mentions similar experiences.

Voigt (59, 60) recorded a *H. schachtii* population which had specialized on hops.

Barley was ordinarily considered to be non-susceptible to *H. schachtii*, and yet Märker (see Baunacke 3, p. 277) mentions the following case. On a field badly infested with this nema, barley was grown for three successive years. The first two years no noticeable injury occurred, but in the third year the crop was destroyed before harvest. This shows that an apparently specialized population may adapt itself in a rather short time to a new host plant and again become injurious.

A large number of similar observations could be added.

Very often the nemas of one and the same species, but from different plots or different localities (sometimes close by) or different countries, attack different crop-plants here and there, so that the same crop will be damaged in one place but left unharmed in another. Potatoes, for example, will be harmed in one field but not in another, even though the harmful nema is present in both places. As in Liebscher's case, the *H. schachtii* populations, in fields and plots which touch each other, will often behave very differently; in one plot they will attack certain weeds heavily, but will leave them unharmed in the neighboring field. Mr. Gerald Thorne mentioned such cases to me from the sugar-beet fields near Salt Lake City, Utah, where in one field *Chenopodium album* would be heavily infested but would be free from attack in the next field. In all these cases the crop-history of a field will probably give the key to an explanation.

It is of practical interest to mention here certain experiences with the trap- or catch-plant method of Kühn. The latter used as catch-plant *Brassica compestris* var. *annua* ("Sommerrübsen") for the sugar-beet nema; Fuchs (19), white mustard (*Sinapis alba*); yet Baunacke (3, p. 239) showed by experiment in Saxony and in Brandenburg that these same plants were

never attacked by some populations of the sugar-beet nemas. In these two cases it could be proved that the nemas were highly specialized on sugar beets, for both populations apparently had lived exclusively on this crop for a great number of generations.

The foregoing examples show how differently various populations of a nema species will behave toward various plant species, all known to be its hosts. Some populations are rather polyphagous, others are monophagous.

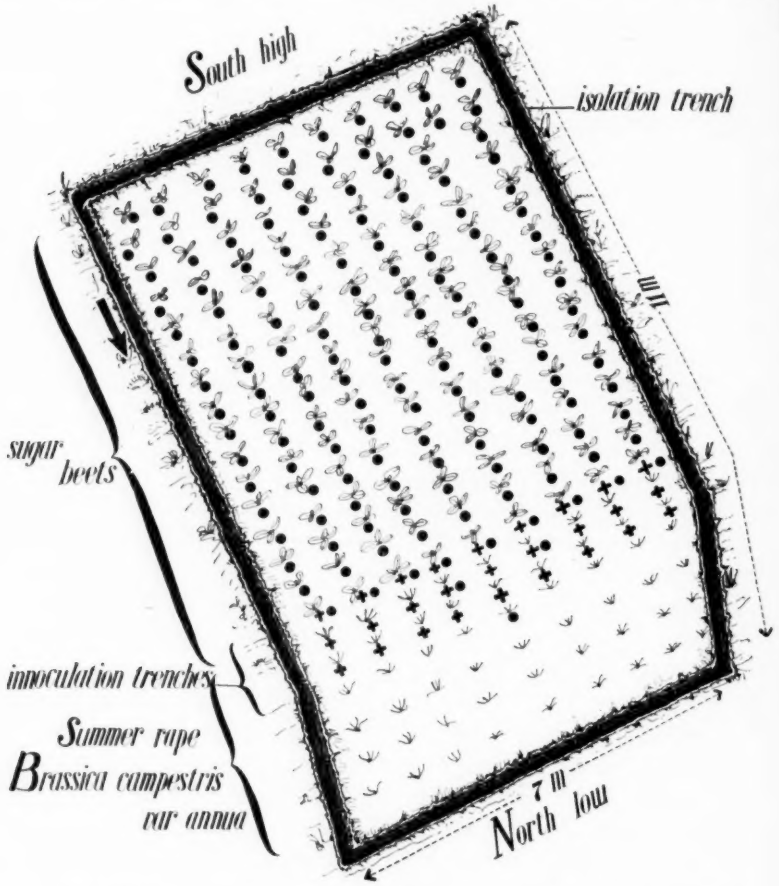

FIG. 2. Schematic representation of a field experiment of Baunacke to show the ability of *Heterodera schachtii* to locate its host plant. The population was apparently highly specialized on the sugar beet and, because it was left to choose, attacked only a few of the summer rape plants, although this is a good host plant and even used as a catch- or trap-plant. The nemas moved against the water flow. (The figure is made following the descriptions and two figures of Baunacke.)

The following example, one of Baunacke's experiments, will show a very astonishing faculty of the nemas, that is, their ability to locate, even at considerable distances, the preferred food-plant.

A plot 7x11m. (see fig. 2) hitherto absolutely free from *H. schachtii* was inoculated with a population of this species of nema, which for many generations had lived on sugar beets. The inoculation was made in November, 1919, in the following way. At the place marked on the schematic figure, three trenches fifty centimeters distant from each other, and thirty centimeters deep, were dug, and the bottom, about hand-high, was covered with soil containing *H. schachtii* and then filled again. To prevent emigration of the nemas, the plot was isolated by a trench of sufficient depth. In the next spring the 1.8m.-long northern part of the plot, including the inoculation trenches two and three, were planted with *Brassica campestris* var. *annua* ("Sommerrübsen"); the rest of the plot, including the inoculation trench one, with sugar beets. The plot inclined toward the north side, which is of importance in regard to the carrying faculty of the soil water which flowed in the direction indicated by the arrow.

As early as June 15th, the sugar beets in the inoculated trench one and in the immediate neighborhood were already infested, whereas the *Brassica campestris* var. *annua* plants in the inoculated trenches two and three were absolutely free. On September 28th, the nemas had already reached the southern end of the plot, whereas a careful examination of the *Brassica campestris* var. *annua* at the inoculation trenches showed only a few plants with a few females of *H. schachtii;* and, at a distance of one meter from the inoculation place, no infested *Brassica* could be found. Yet, as already remarked, the soil water moved toward the latter. This experiment, under free-land conditions, shows very well the ability of the nemas to locate their preferred host plants, even at considerable distances in the soil, and to move toward them in an active way, even against the water-flow.

A case which shows that the same ability to distinguish different plants exists in *Heterodera radicicola*[2] is given by Tischler (56, Figs. 3 and 4). This author found *Circaea lutetiana* and *C. intermedia* growing so closely together that, at the margin, the roots of both species intermingled. And yet he found *C. intermedia* absolutely free from *H. radicicola,* whereas the roots of *C. lutetiana* interminged with the former were infested. If, however, *C. intermedia* were planted in jars with soil from *C. lutetiana* containing the nemas, they would attack it, not having their preferred host at their disposal. This is a splendid example to show that the "botanical instinct" of our nemas enables them to distinguish even closely related plant species.

[2] This form was recently placed in a separate new genus, *Caconema* (see **13**: 118–119).

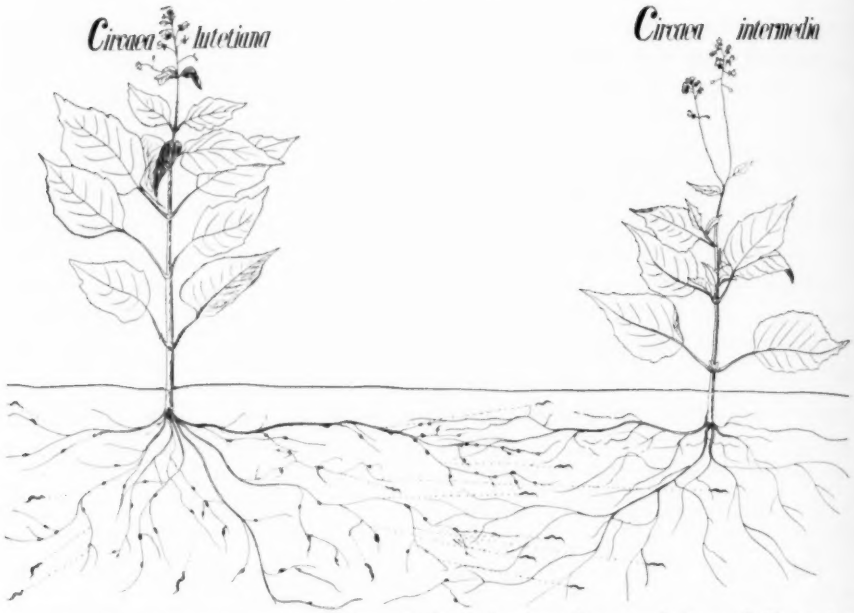

FIG. 3. Schematic representation of the behavior of a population of *Heterodera radicicola* as observed by Tischler. The nemas attacked only the roots of *Circaea lutetiana*, even though these roots were mixed with those of *C. intermedia*; the nemas were able to distinguish sharply both species.

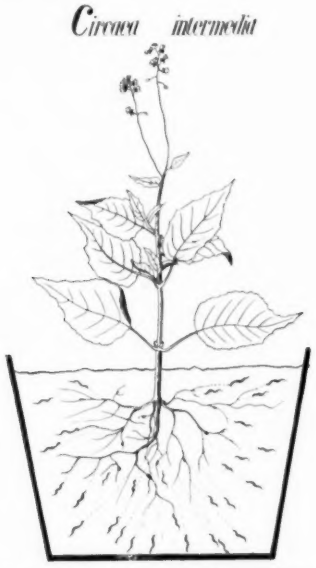

FIG. 4. Schematic representation of the behavior of the same population as in Fig. 3. Since the nemas had no other plant at their disposal, they attacked *Circaea intermedia*, which they had ignored under the previous conditions.

Atkinson (1) found *Amaranthus spinosus* at Auburn, Ala., not attacked by *H. radicicola* even in the neighborhood of badly diseased plants, whereas this same species is reported by Neal (37) as the "most dreaded and destructive agent in the spread of root-knot" in Florida.

But these faculties are possessed not only by the members of the genus *Heterodera;* they are apparently developed also in a similar way in many known plant-parasitic forms. Literature is especially rich in examples concerning *Tylenchus dipsaci,* which form, if taken as a whole, is very polyphagous, but which seems easily to develop populations more or less specialized on groups of plant species or even on single species. The bulb growers of Holland distinguish different strains specialized on certain plants, and Slogteren showed that these strains behaved in a way similar to that described above for *H. schachtii* and *H. radicicola.* As shown by figure 5, schematic sketches of Slogteren's (49) experiments, a *Tylenchus dipsaci* population which has lived on Hyacinths or on Narcissus, etc., will always attack this host first and leave the other plants unharmed. What astonishes us most here is the accuracy with which the nemas locate their preferred host plant.

These few cases are sufficient to show what we want; they could easily be multiplied.

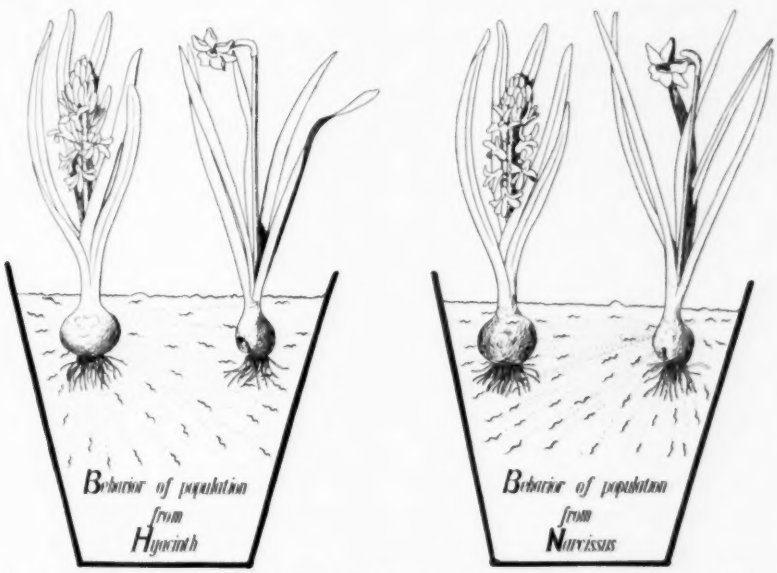

FIG. 5. Schematic representation of the behavior of two different populations of *Tylenchus dipsaci,* as described by Slogteren. The one population lived on Hyacinths, the other on Narcissus. Therefore, if left to choose, the first population will ignore the Narcissus, the second the Hyacinth, for each will attack only the host of its ancestors.

The situation may best be characterized as follows: Although the different species of plant-parasitic nemas attack and feed on a wide range of host plants, a given population of one of these species will, if possible, always first attack the kind of host plant that its parents and ancestors lived on. If this plant is not available, in not being present or in being already highly parasitized, host plants of any kind of near relationship, taxonomical, chemical, etc., will be sought and attacked. If the ancestors of a population of one of the mentioned nema species lived during many generations on a number of different host plants, all these host plants and their related forms will be quite easily attacked. The population will then usually be found to be of somewhat polyphagous instinct. But, if the ancestors of a population have lived for a number of generations on a single species or even variety of host plant, their descendants may not attack any other plant known to be a host; or, if they do so, it will be only with difficulty, and then only in a small number. It might require generations before a new host is again attacked in the same degree as the old one. But a good part of the population apparently unable to accommodate itself to the new conditions starves to death, and in an extreme case only a few specimens, or even none, seem to have the ability to accustom themselves to the new host plant. Such nema populations are monophagous, and because of their specialization on one certain host plant were named "strains" or "biological or physiological races" in analogy to the well-known biological or physiological races or strains in some fungi, insects, etc. Most of the investigators accepted this conception and thought that they had in these nema populations forms with certain strongly inheritable characters. These "strains" played a prominent role in the experiments of all the investigators who aimed to breed so-called nema-resistant plant varieties. But unfortunately their true nature did not seem to be recognized. Nobody has been able, at least up to the present time, clearly to show morphological reasons for the establishment of definite strains, races, or varieties. Moreover, the experiments to reveal sharply cut physiological differences were very contradictory. One investigator could infest numerous plants with a "strain" from a certain plant, and a second investigator with a "strain" from the same plant but from other localities had no results. There are also many contradictions in regard to the host plants: one author states that a plant species is infested with a certain nema species, another one finds that it is not. But, in general, this strain, or biological race, theory was accepted. Only quite recently Baunacke denied the presence of any such races. This shows clearly that the former conception was not a satisfactory one and did not explain the multitude of facts.

In some papers on plant-infesting nemas, lists of highly susceptible crops and plants are often given with lists of others which are only slightly

affected. From the foregoing study it results that such lists may have little absolute value. Apparently any plant said to be only slightly affected by a nema pest may become highly affected if the nema has time to adapt itself and to specialize on this particular host.

Since the behavior of a given nema population toward a host plant is largely dependent upon the nature of hosts on which the ancestors of the nemas lived, many mistakes were made in experiments during the past, especially in those on host resistance, host immunity, and in the so-called susceptibility tests. That something was wrong in the fundamental conceptions of all these experiments could easily be seen from the contradictory results obtained. Observations of one investigator were very often denied by another, as shown below. From the previous section, it can be concluded that any resistance, immunity, and susceptibility experiments with a given nema population may easily be incomplete, misleading, and unscientific, unless the host history of this nema population is known. A few examples from literature will show this.

Ramsbottom (43, p. 54) wanted to test the statement of Ritzema Bos (47, p. 308) that the Narcissus "strain" would not affect onions, but he failed, for the specimens that he took from Narcissus happened to infest onions badly. Why was this so? Ramsbottom unfortunately does not tell us how long his Narcissus "strain" had lived on Narcissus and whether a few generations ago it had been in contact with onions. The knowledge of the hosts for at least a number of immediate ancestral generations, however, seems to me exceedingly desirable, if not indispensable.

He succeeded also in infesting *Scilla nutans* with the same Narcissus "strain," which perhaps is an additional point to sustain our conception that he did not work with a highly specialized Narcissus "strain." Ramsbottom adds to these rather critical statements of the biological-strain theory, however, that on a visit to Spalding he made some contradictory observations. In two instances onions, lucerne, and clover (all susceptible crops) were found growing in close proximity to diseased Narcissus bulbs, but no damage appeared to have been inflicted to the former crop.

We are quite convinced that if Ramsbottom had exposed simultaneously to his Narcissus population Narcissus, onions, and *Scilla nutans*, he would have obtained only infested Narcissus. In the case of his field observations the Narcissus "strain" could choose, and therefore attacked, only Narcissus, and left the onions, lucerne, and clover unharmed.

Perhaps his experiments do not disprove the theory of "biological strains," but possibly if he had had a Narcissus strain which for long generations had lived exclusively on Narcissus, he would have obtained only a low degree of infestation in the onions and *Scilla nutans* that he chose, or even one not at all perceptible.

It is one thing to put an animal in a position to choose its food, but it is quite a different thing to force it to take a given food in order to escape starvation.

Very significant also are some experiments carried out and described by Goodey (22). This author wanted to test the susceptibility of certain crops and legumes for *Tylenchus dipsaci*. He took the nemas from an infected red clover field and gives the folowing table as expressing the "intensity of susceptibility" of the different plants:

Red clover (Canadian)	316	Group 1
" " (French)	215	
" " (English)	190	
Cow grass (Swedish)	167	
Kidney vetch	163.75	
Red clover (Wild English)	160	
Cow grass (English)	38.25	Group 2
Alsike clover (Canadian)	37	
" " (English)	28.5	
Sainfoin	7	Group 3
White clover (Wild Cotswold)	5.5	
" " (English)	4.75	
" " (Wild Kentish)	2	
White clover (Sutton's Mammoth)		Group 4
Lucerne		
Trefoil		

Therefore Goodey concludes that the susceptibility of group 1 is very high, that of group 2 much less, that of group 3 only slight; and group 4 appears to be non-susceptible. But let us quote the final statement of Goodey himself: "The results have a practical bearing of considerable importance to the farmer whose land is infested with *Tylenchus dipsaci*, and whose red clover is therefore liable to attack from this parasite. If he wishes to avoid stem disease, he should not sow red clover, cow grass, or alsike clover, but should make use of trefoil, lucerne, sainfoin, or a large white clover, such as Sutton's Mammoth White."

Yet lucerne (alfalfa) sometimes is one of the crops most badly affected by *T. dipsaci*. How can this be true considering Goodey's results? The nemas used for his experiment were taken from a red-clover field and apparently he had a population of *T. dipsaci* rather highly specialized on red clover, which very well explains the results of his susceptibility tests in the light of our conception. His conclusions would be all right if he would make the reservation that they are for such a specialized population of *T.*

dipsaci, but Goodey is certainly too hasty in generalizing such conclusions for *T. dipsaci* as a whole. We are convinced that this red-clover population of the present nema would soon have adapted itself to lucerne and other host plants. To recommend in this case host plants not susceptible to the specialized red-clover population, and of annual nature would have been perfectly safe, but certainly not lucerne and other hosts of perennial nature. This perennial nature would be the best opportunity for the nema to adapt itself, and perhaps in two or three years lucerne (alfalfa) would be highly infested.

The previous example shows well how the advocated conception explains observations and facts of hitherto rather puzzling nature, and gives more definite lines along which to work in crop rotation.

These examples may be sufficient to show one reason why so much of the endeavor of a series of investigators to find and to breed nema-resistant crop varieties had not yet produced the desired results, even after about thirty years of experimenting. The fundamental conceptions upon which these experiments were founded were inadequate. The terms "strain" and "biological race" were also often used in a very inexact and unscientific way. It is not allowable, for instance, to call a population of *T. dipsaci* a "strawberry strain" just because these nemas were found on strawberries. Before doing this it should be ascertained how long this population had really lived on strawberries and to what degree they were specialized on them. It is very incorrect so to name it if the specimens of the population also attack alfalfa, red clover, potatoes, buckwheat, peas, onions, etc. It seems to me that only a population which for many generations has lived exclusively on this plant and is therefore specialized on it should be so termed. But if the host history is not known, and experiments do not prove a strong specialization on strawberries, the term "strawberry strain" is certainly misused. A strain is, indeed, something more stable, at least as the term is used in genetics. It is of no value to state that the "alfalfa strain" of *T. dipsaci* can be brought to infest red clover, buckwheat, alsike, white clover, peas, turnips, potatoes, and Polygonum, if the former host history of this "alfalfa strain" is not known. In this host history of the "alfalfa strain" lies the explanation of its present behavior, and from a knowledge of this host history, one might even be able to predict behavior toward new host plants. Such "alfalfa strains" of different origin and unknown host history might behave quite differently and the results of such experiments would lead only to confusion. The behavor of these "strains" seems to be very largely a function of their host history—of the time they lived on a certain plant; and, as experience proves, it is therefore something very variable.

The conclusion therefore is that all experiments on nema resistance, immunity, and susceptibility of plants should be made only with populations

of which the host history is well known for at least a number of generations. It is very doubtful whether a nema population of *Heterodera radicicola,* for instance, could be found, of which the present members could be brought to attack all the different plant species known to be its hosts.

However, it would seem possible to attract the offspring of a nema population of *H. radicicola,* for example, to all the known host plants by changing the host for the succeeding generations so that each following host would be of the closest possible relationship to the foregoing one, and to try in succession all the known hosts. Perhaps it would be possible in following this same line to infest a large number of plants not yet known as hosts.

Another point of practical use results from the preceding deductions, namely, that any crop variety should be claimed to be nema-resistant or immune or non-susceptibile only after this crop has been brought into contact, for at least a number of years, with a nema population which has lived in large numbers on a crop variety closely related to the one being tested. As we understand the situation, a nema population may adapt itself to a new host little by little, and only after some time be truly specialized on it. No statement that a crop variety is nema-resistant can be fully accepted until the host history of the nema population with which the experiments were made is properly known and stated.

The application of the present findings may be of some importance in crop rotation also. Usually it is said that any so-called nema-susceptible crop should be left out of the crop rotation on infested fields. However, as results from the previous sections show, it might in many cases be perfectly safe to use annual crops known to be hosts of the infesting nema species, as, for example, in the case described by Liebscher (30) and mentioned above, it would have been perfectly safe to grow sugar beets on the plot where *Heterodera schachtii* has damaged the peas so badly. A summer's crop of sugar beets would not have suffered from that *H. schachtii* population which had lived on peas for so long a time. On the plot where oats were so badly infested with *H. schachtii,* peas would have been safe.

For combatting nemic pests by scientific crop rotation, one has to know the host history of the nema population in a field (not only the crop raised but also the weeds present every year) and, armed with this knowledge, one may use even crops susceptible to the species of nemas in the field, but not to the present population.

HOW ARE THE NEMAS ABLE TO RECOGNIZE AND SELECT THEIR HOST PLANTS

The facts revealed in the foregoing show clearly that our plant-infesting nemas have the faculty of recognizing a host plant and even of distinguishing a preferred host plant. The preferred host plant seems always to be that one upon which the ancestors of the nema population lived. The degree

of preference for a certain host plant seems to grow with the number of successive generations a population of a nema species has lived on it; and the more the nema specializes on one host plant, the more it will apparently lose the ability to attack other host species, and the more finely developed will its sensibility for this one preferred host become (3). Now the question arises as to the causes of this significant behavior. Are they within the plant, the nema, or within both?

Baunacke (3) showed that the nema is led to its preferred host plant by some chemotactic influence exerted by the plant. His experiments seem to prove that some kind of root secretions, chiefly formed by young growing roots, are carried by the soil water to the nemas, which, stimulated by this substance, even leave the egg shell or the cysts, a fact recently developed further by Rensch (45) in some very interesting and promising experiments. Moving towards the higher concentration of the dissolved substance they find their host. It has to be assumed from these experiments that the active root secretions of different plants must be different and that the nemas are capable of recognizing the differences and of choosing those of the preferred host plant first.

However, taking into account the more recent experiments of Rensch, it seems at first that the active part of these root secretions is of a rather simple chemical nature. Rensch confirmed the results of Baunacke that washings of the roots of growing sugar beets, containing the active parts of the root secretions in solution, would stimulate the larvae contained in the brown cysts of *Heterodera schachtii* to hatch. Rensch was even able to get the same results by the application of two synthetical products, named A and B, prepared by a chemical firm. What he says about their chemical nature is that the first, A, is a known stuff from roots of many plants and that the second, B, is formed by the transformation of plant plasma in the soil. It therefore seems that these active compounds must be of a rather simple chemical nature. But, if we compare these results with all the facts of the ability of the nemas to respond to and to distinguish the stimuli of different plant species and even varieties, it seems impossible that these compounds are the only directing stimuli. From the results of the experiments of Rensch and a study of the behavior of plant-parasitic nemas toward their hosts, I rather conclude that the compounds which stimulate the nemas to hatch are not identical with the ones which direct them afterwards to their preferred host plant. Compounds generally formed by the growing of roots and of little or no specific character might act like first messengers on the encysted larvae of the nema and announce to them that conditions for leaving the cysts were good. Naturally the larvae will move toward these stimuli, because they are signs of plant life, but the final selection of the host seems to me to be directed by compounds of more specific nature.

This conception seems also to be supported by the action of chicories upon the sugar-beet nema. Several authors proved that these plants stimulate to a high degree the hatching of the larvae in the brown cysts, but no nemas or very few will attack it.

In showing the chemotactic influence of the plant upon *Heterodera schachtii*, Baunacke, and later Rensch, made a most important step toward an understanding of the mutual relationship of host and parasite. Without doubt similar conditions are present in *H. radicicola*, *Tylenchus dipsaci*, and other plant-infesting nemas and their hosts. The nemas must have means to recognize and distinguish their hosts through chemicals secreted by the latter and carried by the soil water. The nature of the active root secretions is not yet known, but must doubtless be very specific for each plant species, sometimes even for plant varieties or races. Neither Baunacke nor Rensch traced these relations any farther. The nema, as the perceiving organism, was not studied more closely by them; they seemed to be satisfied with the establishment of the relationship. Yet, for a true understanding, we need to know how the nema is able to perceive the chemical stimuli sent out by the plants. Has the nema organs of perception for such stimuli? Undoubtedly these organs can only be sense organs. Furthermore, they must be placed near or at the head end. If not, they could never guide the nema toward its host. The head end of the nemas, in fact, shows at least two, sometimes three, groups of sense organs differing decidedly in structure and undoubtedly also in their functions. These are, first, the so-called head, labial, and mouth papillae, which are thought to be organs of touch (tangoreceptores); second, the amphids, or lateral organs, which by zur Strassen (55) and the writer (50, 54) have been claimed to function as chemical sense organs (organs of taste, gustoreceptores); and third, in some marine and fresh-water free-living forms there are also organs for the perception of light (ocelles, photoreceptores).

The amphids, or lateral organs, are, as the writer thinks, doubtless the sense organs with which the nemas perceive the chemical stimuli which Baunacke and Rensch in their experiments proved to be sent out from the roots of sugar beets.

These amphids are well known to all investigators who have worked on free-living nemas. They were first named lateral organs by Bastian (2), because of their constant lateral position. Only exceptionally are they shifted slightly dorsal. They were later renamed amphids by Cobb (12) because animal morphology had already lateral organs in fishes, amphibians, etc.; also, and more important philologically, the nemas have many other organs that are "lateral." There is no doubt that they are not homologous with the former, and it was therefore thought best to rename them. Until quite recently amphids were assumed to be a feature of only

some free-living genera. Investigations, chiefly by Cobb and the writer, showed that they are present also in many parasitic forms from widely separated groups. As they were found in any nema which was closely searched, it might be safe to say that they are present in all nemas, and are their most characteristic and typical feature. Textbooks could safely assume this character to be typical in their diagnostic descriptions of nemas, if once they would try to become modern in this respect and not offer again and again chapters on nemas written exclusively about a few parasitic forms, neglecting the bulk of the group in all its morphological and physiological richness.

Years ago zur Strassen (55) pointed out that the so-called lateral papilla, as described by authors of parasitic nema papers, might be homologous to the amphids. Again and again investigators showed that these so-called lateral papillae were entirely different in structure from the submedial ones, and the presence in them of apparently glandular cells connected with nervous elements was repeatedly stated.

Recent investigations of Cobb (13) showed the presence of these amphids in *Heterodera radicicola*, and the present study attempts to describe them also for *H. schachtii*, *Tylenchus dipsaci*, and *T. tritici*.

It may be repeated here that Baunacke was not the first who observed such pronounced chemotaxism in nemas; similar observations were made by a number of other investigators such as Buerkel (9), Marcinowski (33), etc. Having adopted the views of zur Strassen about the assumed chemical function of the amphids, the writer himself has called attention to this in many of his previous papers (50, 51, 52, 53, 54).

It is of special interest to know that these organs are also present in *Heterodera schachtii*, because it is for this form that the chemotaxic relationship between plant and nema has been proved experimentally by Baunacke. Here the amphids have the usual lateral position, and are somewhat difficult to see; this is the chief reason why they have been overlooked in the past. The amphidial opening is very close to the mouth opening (Fig. 6C) and has, as seen from the front, a somewhat oval shape. A narrow canal leads into a long conical structure which can be followed for a distance towards the nerve ring. Just behind the spherical swellings on the inner end of the spear, the cavity of the organ appears to be closed, so that the cephalic part seems to form a pouch-like structure, inside of which a small number of threadlike fibers can be seen. These are apparently terminals of a bundle of nerve fibers. The cross sections represented in figure 6 (D and E), combined with figure 6 (A and B), enable one to get a conception of the organ more or less approaching the reality. The writer is inclined to assume that, as in other nemas, a cell of apparently glandular nature surrounds the nerve fibers, connecting the terminals with the central

nervous system, and that this cell begins right where the amphidial pouch is closed.

Cobb (13), as mentioned above, recently described a very similar structure for *Heterodera radicicola*.

Also *Tylenchus dipsaci* proved to have these amphids, as shown in figure 7 (A–D). A front view is given in figure 7C, and the openings of the am-

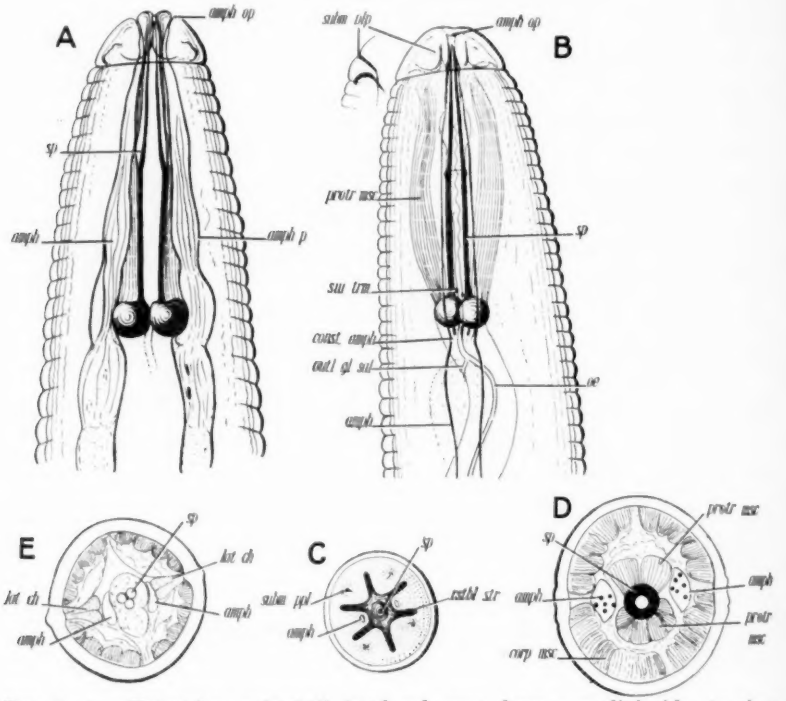

FIG. 6, A. *Heterodera schachtii*, head-end, seen from a medial side, to show the amphid on each lateral side; *amph*, amphid; *amph op*, amphidial opening; *amph p*, amphidial pouch; *sp*, spear.

B. *Main fig. Heterodera schachtii*, head end, seen laterally; *left small fig.*, sketch of a submedial head papilla as seen in profile view; *amph*, amphid; *amph op*, amphidial opening; *const amph*, constriction of the amphid, apparently the place where the amphidial pouch ends; *oe*, oesophagus; *outl gl sal*, outlet of the salivary gland; *protr msc*, protractor muscle of the spear; *sp*, spear; *subm ppl*, submedial papillae; *sw trm*, probably a swelling in the terminal.

C. *Heterodera schachtii*, front view of the head; *amph*, amphid; *sp*, spear; *subm ppl*, submedial papillae; *vstbl str*, vestibular structure.

D. *Heterodera schachtii*, cross section through the head in the region of the cylindrical part of the spear; *amph*, amphid; *corp msc*, body muscles; *protr msc*, protractor muscles of the spear; *sp*, spear.

E. *Heterodera schachtii*, cross section right behind the bulbs of the spear; *amph*, amphid; *lat ch*, lateral chord; *sp*, spear.

phids are easily distinguished from the four submedial papillae. Other aspects of the organ are shown in figure 7A; a somewhat sublateral view, figure 7B; a medial view showing the organs in profile in figure 7D, where a cross section is drawn. In the specimens of this species, swellings of the terminals, as described by Cobb for *H. radicicola*, could be seen, and the whole structure of the organ was even better recognizable than in the foregoing *H. schachtii*. These are, however, apparently results of the fact that the specimens of *T. dipsaci* which were used for the present study were adults, whereas those of *H. schachtii* were still in the young larval stage, therefore much smaller and more difficult for the study of details.

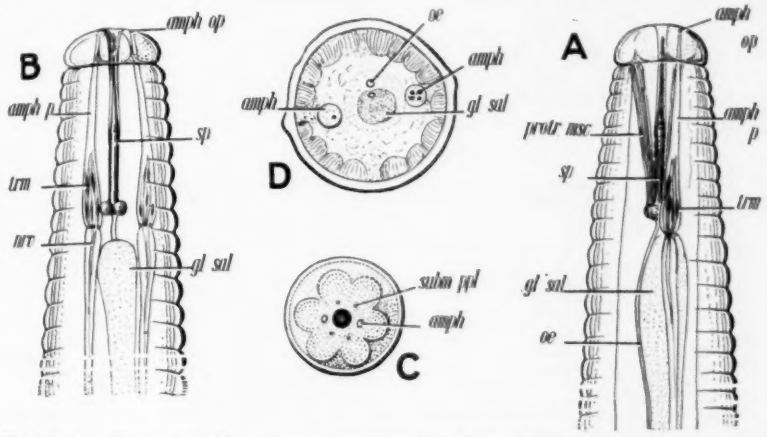

FIG. 7, A. *Tylenchus dipsaci*, ventro-submedial view of head end; *amph op*, amphidial opening; *amph p*, amphidial pouch; *oe*, oesophagus; *protr msc*, protractor muscle of the spear; *sal gl*, salivary gland; *sp*, spear.

B. *Tylenchus dipsaci*, ventral view of head end; *amph op*, amphidial opening; *amph p*, amphidial pouch; *nrv*, apparently amphidial nerve fibers; *sal gl*, salivary gland; *sp*, spear; *trm*, terminals.

C. *Tylenchus dipsaci*, front view of the head; *amph*, amphid; *subm ppl*, submedial papilla.

D. *Tylenchus dipsaci*, cross section through the region behind the spear; *amph*, amphid; *gl sal*, salivary gland; *oe*, oesophagus.

In *Tylenchus tritici* the amphids are very similar to those of *T. dipsaci* and of the two species of *Heterodera*. A front view shows two circles of head sense organs; the inner circle comprises very fine and minute mouth papillae. There are apparently six faintly developed lips (Fig. 8A), and the lip region is somewhat set off. The submedial lips bear each a very fine cephalic papilla, more easily seen in a front view. The lateral lips, however, seem to be without any papillae but to bear the amphids. In a front view they closely resemble the submedial papillae, but intra-vitam staining shows the difference in structure very quickly. The amphidial openings are

apparently placed on the apex of the lateral lips, and are therefore located in the same circle with the submedial papillae. A very narrow duct leads inward and gradually widens to what might be termed a long, conical, or better, a somewhat irregularly shaped, spindle-like, amphidial pouch with thin walls. This pouch seems to end in about the double length of the spear behind the head end, as indicated by a constriction, after which a more compact part follows. Within the pouch the same elements as in both species of *Heterodera* and *T. dipsaci* could be seen, but it is very difficult to ascertain the number, exact shape, and position. The cross sections as shown in figure 8 (C and D), combined with the views of figure 8 (A and B), may help to present the structures in the best possible way.

If we look for organs of similar structure throughout the animal kingdom, so-called chemical sense organs (taste and smell) of other forms are the first to be considered, as, for example, the taste buds of mammals or insects, etc.

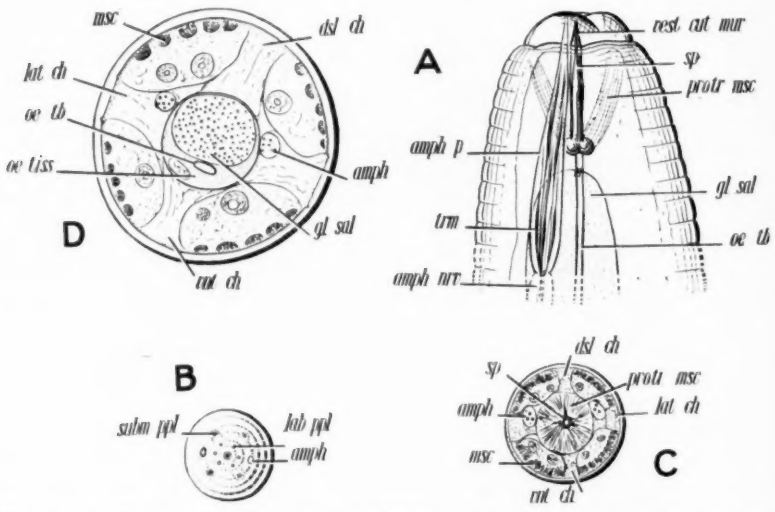

FIG. 8, A. *Tylenchus tritici*, dorso-sublateral view of the head end; *amph nrv*, amphidial nerve; *amph p*, amphidial pouch; *gl sal*, salivary gland; *oe tb*, oesophageal tube; *protr msc*, protractor muscle; *sp*, spear; *trm*, terminal; *vest cut mur*, cuticularized wall of vestibulum.

B. *Tylenchus tritici*, front view of head end; *amph*, amphid; *lab ppl*, labial papillae; *subm ppl*, submedial papillae.

C. *Tylenchus tritici*, cross section through the region of the spear; *amph*, amphid; *dsl ch*, dorsal chord; *lat ch*, lateral chord; *msc*, body muscles; *protr msc*, protractor muscles of spear; *sp*, spear; *vnt ch*, ventral chord.

D. *Tylenchus tritici*, cross section through region behind the spear; *amph*, amphid; *dsl ch*, dorsal chord; *gl sal*, salivary gland; *lat ch*, lateral chord; *msc*, body muscles; *oe tb*, oesophageal tube; *oe tiss*, oesophageal tissue; *vnt ch*, ventral chord.

We have not yet established the connection of the above-described end apparatus of the amphids with the central nervous system. It will be done later; but as this connection has been studied and found to exist in a number of nemas from widely separated groups, and to be of similar structure throughout, the acceptance that the present forms make no exception is certainly permissible. In all probability our parasites do not differ in this point from the typical organization found to be valid for Ascaris (21), Oxyuris (34), Sclerostomidae (31a), Ancylostoma (31), Siphonolaimus (55), Oncholaimus (18), Mermithids (23), etc.

It might be said that we have not yet the experimental proof of the chemical function of the amphids or lateral organs, especially in the present species. This proof will be a very difficult one technically on account of the small size of our parasites and the much smaller size of the organs themselves. To make these organs functionless, and then to study the behavior of an animal deprived of them will be a difficult proposition. Perhaps some free-living marine forms with large-sized amphids could best be used for such experiments. But while experimental proof of the nature of the function of the amphids of nemas is still lacking, there are a number of reasons which speak plainly for their chemical function.

1. Their structure is most often very similar to that of the chemical sense organs of other animals (organs of taste and smell), especially to the taste buds.

2. The amphids show, within the nematode group, a multitude of different forms for which only the conception of their chemical function seems to give a satisfying explanation. In assuming for them a statical or auditive function, however, this structural richness can not be understood; gravity can not be thought to affect differently the various species of one genus or the varieties of one species. And yet the amphids often show marked structural differences even in very close systematic groups. Neither can the conception of their auditive function be satisfactory in view of the apparent specificity of the amphids in each variety, species, and genus. Even if we assume that the environment of nemas is filled with sounds, we are unable to see a relation of specific environmental sounds to the nemas; we can not see any benefit to the nema in perceiving these sounds, and nature never works along lines of uselessness. Neither can any other kind of mechanical waves or pressure explain in a satisfactory way the structural richness of the amphidial organs in our nemas.

3. Numerous cases of so-called sexual dimorphism are recorded in the amphids of nemas, the ones of the males very often being larger than those of the females. Only the conception of their chemical function furnishes a satisfying reason. If they were auditive in their function such sexual dimorphism could only be understood by the conception that the sexes produce

tunes to attract each other and that these tunes are specific for even varieties of species. But no tune-producing organs are known in our nemas. Nor can the assumption of a statical function or a mechanical wave-perceiving function explain this dimorphism.

4. The amphids are probably, without exception, a compound organ of nervous elements with what seems to be a gland. Here, too, the conception of a chemical function seems the one most in accord with this union of organ elements.

5. That the nemas must have chemical sense organs is experimentally proved. If we review all the known sense organs of the nema body, the amphids are, it seems to me, the only ones which could be considered as such, as the structure or position of all others is of a nature which contradicts their identification as chemical sense organs.

6. It is a rule that the amphids of nemas living free in fresh water and sea water are most often of a comparatively larger size (e.g., the end apparatus) than those of the parasites and of the free-living soil forms. This can easily be understood from the conception that the amphids are chemical sense organs and that in the sea and lakes naturally the active chemicals are dissolved more than, for example, in intestinal fluids or in the soil water. The larger size of these organs in fresh-water and sea nemas can easily be explained by this conception.

Thus it seems that many facts speak for this conception, and, so far as I know, none against it.

With the foregoing facts and interpretations which have just been set forth, the whole mechanism of host selection of the plant-parasitic nemas is satisfactorily outlined in its chief points and may be described as follows: Apparently some very specific chemical substances are produced by the growing roots of plants, and are dissolved and carried by the soil water in various directions. They act as stimuli on the nemas, the latter having receptors for them, presumably the so-called amphids or lateral organs on the head end. By moving toward points of higher concentration of the solution, e.g., towards quantitatively higher stimuli, the nemas locate their hosts. The amphids as perceiving organs are highly sensible to the qualities as well as quantities of the acting chemicals.

THE HOST SELECTION OF NEMAS PARASITIC IN ANIMALS

The question arises whether the host selection in nemas parasitic in animals is similar to that here described for plant-parasitic forms. Undoubtedly this might be so in many cases, at least in those where the parasites actively move toward the host. It might not be so in all cases where infection goes on in a more or less passive way and is built upon coincidences

entirely uncontrolled by the nema. As far as the writer knows, different tropisms have already been claimed to be factors playing an important rôle in the location of their hosts, or special organs of hosts, by certain parasites. For example, special stress is laid on the thermotropism of the hookworm larvae. However, it seems to the writer that temperature cannot be the only directing agent. Plant-parasitic nemas also have their optimal temperature and move toward it and show therefore a thermotropism similar to that of the hookworm larvae, and yet it would be a mistake to say that thermotropism is the leading agent in host selection in this case.

It is the so-called histotropism (8, 20) of parasitic nemas which is apparently a result of a mechanism similar to that here described as the host selection mechanism of plant-parasitic nemas. This histotropism, resulting in the finding of their special host organs or host tissues by the parasitic nemas, is undoubtedly a chemotropism and the managing sense organs are assumed to be the amphids. A very definite host-tropism for certain Mermithidae will be described in a paper now in preparation.

It seems also that for certain nemas parasitic in animals, host specializations occur similar to those here described for the plant parasites. Although the matter has not yet been studied along the lines followed in the present paper, there has been much argument and discussion with regard to the identity or systematic difference of some *Ascaris, Belascaris,* and *Trichuris* living in man and domestic animals. Some investigators regard the specimens from different hosts as different species, and others do not. The situation here is not so explicit as in the plant-parasitic forms, and will still need much enlightenment. Some statements about the possibility of the transmission of a parasite from one host to another are rather contradictory, and the situation, as presented today, recalls clearly what has been said about the behavior in this respect of plant-parasitic forms (4).

THE FOOD SELECTION OF FREE-LIVING NEMAS

Comparatively few species of free-living nemas have yet been reared and are more or less known in their feeding habits. Most of these known forms are saprophytic or saprozoic feeders; a good part of them live on bacteria and their products. It is usually thought that these saprophytic and saprozoic forms can easily be reared on almost any kind of decaying organic material. Yet, anybody who tries to rear these nemas may gather experiences of a nature similar to those described in connection with the behavior of plant-parasitic nemas in choosing their hosts. Sometimes the initial culture of one of these nema species is rather difficult; they seem not to be in their optimal conditions; many may die, and only a few finally adapt themselves to the new conditions. After this the culture will go on beautifully; but if again a new kind of food is used, very often new difficulties will de-

velop, which, however, will only last until the nemas have again adapted themselves to this new food.

We gathered some evidence of this kind in connection with *Cephalobus subelongatus* Cobb, a polyphagous species, and yet if we changed the food, after having given a certain kind for a long period, there was always a stop in the development of the cultures. Furthermore, we made similar observations with cultures of many species of *Rhabditis, Diplogaster,* and other *Cephalobi,* etc. We could also quote statements of the same nature from literature, as, for example, Potts (41) and Gilbers E. Johnson's (27) study of the nemas of the common earthworm. Here too the same food for a long period, e.g., for several generations, seems somewhat to specialize the nemas living on it in a way similar to that recorded above for plant-parasitic nemas.

HOST SELECTION AND HOST SPECIALIZATION IN OTHER ANIMAL GROUPS COMPARED WITH THAT OF PLANT-PARASITIC NEMAS

It is not my intention to give here an extensive review and discussion of all the known facts; my aim is only to recall certain outstanding examples which are rather parallel to the situation here treated. Unfortunately the host selection mechanism of most of the lower invertebrate parasites which locate their hosts in an active way has not yet been studied. In higher invertebrates, such as insects, etc., the rôle of organs of scent (smell or taste) is well known and is often wonderfully developed. There are examples of host selection which can be fully paralleled to that of the plant-parasitic nemas (15, 57). We refer in this connection to an interesting paper of Craighead (14) which describes the behavior of a series of Cerambycid beetles toward different host plants, based on extensive experiments. The host-selection principle, as defined by Hopkins (26, p. 353), that an "insect species which breeds in two or more hosts will prefer to continue to breed in one to which it has become adapted" can certainly also be applied to the plant-parasitic nemas, as previously shown.

The host specialization of certain Protozoa, Helminths, and Arthropods parasitic in man has recently been discussed by Chandler (11) to whom we may also refer for more literature. Chandler shows that conditions similar to those of the plant parasites here described are also found in mites and lice, in tapeworms, trypanosoms, and trichomonads, in Rickettsia-like organisms, in spirochaetes, and bacteria. There is everywhere this one problem of the systematic relationship of forms living in different hosts, differing from each other very slightly, or not at all, morphologically, but varying in infectivity for different hosts. But in all these examples from other groups the situation is not yet so clear as in the plant-parasitic nemas. In the latter we already know the identity of all these forms specialized on

different hosts, whereas this identity is still in discussion in connection with the above-mentioned cases of insects, etc. The actual situation as it exists is not so little known here as there, and the plant parasites offer a much better field for investigations of the host specialization problem in general than any animal group. The problem is of highest importance, not only for parasitology in all its branches, but also for all parts of biology, applied as well as theoretical; this may be discussed in the following section.

CAUSES AND THEORETICAL SIGNIFICANCE OF HOST SPECIALIZATION

Undoubtedly the factors which are at work in bringing about all the changes (physiological and morphological) that a parasite shows in its adaptation to a new host, and in its specialization to different hosts, are of similar nature in all animal groups previously mentioned. Each new or different host represents a change in environment. All investigators agree that at least physiological changes take place, and it seems evident to me that these go hand in hand with morphological changes, although they are often hard to perceive. There are indications of morphological differences in some "strains" of our plant parasitic nemas, but they have never been studied with enough exactitude. Do these changes take place before the parasite reaches the new host, or are they a result of the new environment? Chandler in his interesting paper (11, p. 334) discusses this matter and lays much stress upon a possible segregation and survival of favored genetic races but does not see in this process the only possible way; somatic acclimatization, induction, and preinduction in his opinion, although of less importance, are still processes which nature may use here.

Chandler goes even further: he sees in the formation of many geographical and ecological races of species the same factors at work as in the process of host specialization. Very little is known about the true nature of the process, but what is known certainly puts this phenomenon close to that of host specialization.

The same author in this connection also discusses the so-called drug resistance or what Ehrlich (17) termed "Giftfestigkeit" of the lower organism. Here too, it seems to me are similar factors at work. If a certain population of these organisms can be accustomed step by step to otherwise deadly toxic substances, this phenomenon at least greatly resembles, or is perhaps identical with, the adaptation of some parasite to a new host and the gradual specialization on a certain host as shown in our nemas and as expressed in Hopkins's principle applied to insects.

The problem involved here is that of the ability of the living matter to respond to outside stimuli in an adaptive, regulative way. But it is not our intention to discuss here this question which is already fully dealt with in many other papers. The plant-parasitic nemas are exceptionally good sub-

jects for the study of the whole problem. The situation, at least with regard to the metazoa, is here, as already stated, more explicit than anywhere else. The chief point is the fact that the changes begin with the host-selecting mechanism. As shown in previous sections of this paper, progressive host specialization in our plant-parasitic nemas begins with a progressive faculty of recognizing a preferred host, of answering the stimuli from this host in a more and more accurate way, and of being more and more sensitive to these very stimuli. At this time the parasite is still outside the preferred host and therefore not yet subject to its full environmental influences; this makes the phenomenon still more astonishing but points to a definite way of how the changes for specialization take place. The perceiving apparatus of the chemical sense organs is first involved and shows, it seems, the most outstanding changes.

There are several possible explanations. Have we here an exclusive nervous action? Are the sense organs and the conducting system only involved in the changes in that a certain kind of stimulus is more easily perceived by its repetition? Have we here a kind of ability to learn?

In the whole process one is led to see simply a result of selection. If we assume that in a somewhat polyphagous population a number of food strains are contained, then the gradual specialization on a certain host plant would be brought about by a more and more strict selection. But this explanation does not seem to me entirely satisfactory. It would be necessary to assume that even in the highest specialized population specimens of still impure genetical constitution are present from which strains of any kind could be segregated, and cases like those observed by Tischler (56) could hardly be understood. Here, if left to choose the host, the entire population goes to *Circaea lutetiana*, and no specimens to *C. intermedia*. But if there is a lack of the former, *C. intermedia* is well attacked. If selection were the only and the chief agent, this process would not go on in the manner observed; a number of specimens would certainly go to *C. intermedia* in Tischler's case where there was a choice, and it seems to me that the very same number of nemas, and no more, ought to be found on *C. intermedia* in the second alternative. Any such experiment of free choice of food and forced food should result in the same Mendelian segregation. However, since this is not the case, it seems to me to disprove the conception that selection is the chief factor.

But still another line of thought for explanation and understanding of the phenomenon might be considered. The nervous end apparatus, by the generation-long action of the same quality of a stimulus, seems to lose the ability to respond to any other quality; therefore it could be thought that the assumed ferments in the amphidial fluid get more and more adapted to the specific stimulus of the one host plant as the digestive ferments answer

the nature of the food taken in. This would mean that the glandular cell, supposed to be always connected with the nervous elements, would, by generations of life on the same point, lose the capability of changing the quality of the ferment. Or does the nature of the food, after the first step in adaptation to a new host is once made, influence the supposed amphidial ferments in a parallel direction?

The whole situation, as described above, reminds one much of the behavior dogs show toward game animals. Some are specialized on rabbits, others on foxes or some other specific game, and still others take up all kinds of game.

THE HOST SELECTION AND HOST SPECIALIZATION PROBLEM IN ITS APPLICATION IN THE STUDY OF NEMIC PLANT PESTS

The facts and viewpoints described and discussed in the foregoing sections are doubtless of much practical significance, at least in the study of nemic plant pests. Several well-separated problems can now be seen; to distinguish between which is undoubtedly of value. There is first the problem of the attraction, non-attraction, and repellancy of nemas by plants. As a second problem comes that of the resistance of hosts toward the attacks of nemas. Here the nemas are attracted by the host, but mechanical, chemical, or other obstacles prevent them from entering. A third problem is that of host immunity. Here the nemas are attracted by the host and are able to enter it and live in the host, but apparently do no perceptible harm to it.

The Problem of Host Attraction, Host Indifference, and Host Repellancy

At various places we have already called attention to the value of the knowledge of the host selection problem in control of nemic pests in plants. The problem divides itself into the three subproblems named in the title of this chapter. Of these, host attraction and host indifference are closely related to each other. It is needless to repeat what has already been said about the importance of a thorough knowledge of host attraction and host indifference for any application of Kühn's trap-plant method or the "Reizpflanzenmethode" of Baunacke or crop rotation. Host attraction and host indifference are phenomenona of very variable nature. Although future investigators may have to solve numerous question, these following points are regarded as somewhat ascertained.

1. Host attraction and indifference are not only the result of the specific constitution of a plant, but also of the host history of the immediate ancestors of the nema.

2. The choice of a catch- or trap-plant, that of a "Reizpflanze," and that of a crop in crop-rotation control methods has to be based upon this host history of the nema population to be controlled.

3. Perennial plants, even though they are not yet known as hosts, should rather be excluded from crop rotation in nema-infested fields, as any nema population having the same plant at its disposal for generations may adapt itself to it.

4. In crop rotation on nema-infested fields, not only the crop history, but also the nature of the weeds present each year has to be known and considered in the choice of a suitable crop.

5. In irrigated land, hitherto it was thought that the nemas were spread by the carrying capacity of the soil water. After the experiment of Baunacke mentioned on p. 503 and after we learn that the soil water is transmitting the attracting chemical stimuli from the plants to the nemas, this problem gains a more complex aspect. Water flowing from uninfested fields to infested fields must direct the nemas of the latter to the former if the same plants, or even more preferred ones, grow there. Naturally this is true only of the water flowing in the soil itself, and not of that of the watering channels.

If an isolation and determination of the chemical substances which act as attracting stimuli upon the nemas could be made, the way to the use of baits would be more easily approached, and perhaps more economical and efficacious methods than the catch-plant method of Kühn could be found. A recent publication by Rensch (46), as already mentioned, opens wide possibilities along these lines.

With regard to the third sub-problem here touched upon, that of host repellancy, there are very few facts known. Chicory and onions are said by some authors (25, p. 8; 29, p. 334; 35, p. 1007; 36, p. 89; 64, p. 8) to act in a way which at least partly resembles repellant action.

If plants could really be found which are repellant toward the nemas above mentioned, it would not seem impossible to find out the cause, and perhaps the chemical, which acts as such.

Hitherto investigators have been most often endeavoring to find chemicals to kill the nemas in the soil. Although hundreds of different preparations were tried, no very satisfactory result was obtained. A search for repellants has not yet been made. Perhaps such fluids could also be found for plant-parasitic nemas, as the anthelminthics used for removing *Ascaris* (Santonin, Chenopodium) or hookworm (carbon tetrachlorid) are perhaps repellants, and not killing fluids. The ideal arrangement would be to have a repellant which would be highly parasitotrop (17) and would act at the same time as a fertilizer on the plant so that its repeated application would result in a doubly beneficial influence on the plant.

The Problem of Host Resistance

In the past, investigators spoke very often of host resistance in cases where non-attraction would have been the right term. A plant can only

be termed resistant if it actually resists the attacks of the nemas. But if the latter do not attack it because they do not perceive its presence, such a condition can hardly be called resistance. In the study of plant-parasitic nemas, the resistance of a plant means that it opposes the entrance of the nemas by some mechanical or perhaps chemical means. The use of resistance in this restricted sense is not only more appropriate in the existing situation but also helps to separate the wide problem of mutual relationship of plants and nemas into smaller parts with more definite questions and more sharply outlined points of attack. Heretofore, if a plant was not found to be infested, it was termed resistant, regardless of the causes, which often were not at all within the plant.

A plant may resist the attacks of nemas either by some mechanical or chemical means. Unfortunately very little is known with regard to this. There are a few definite cases of apparently real resistance mentioned in literature (62, 32, 39, 63).

Only for cowpeas, as far as the writer knows, was an attempt made to find out the cause of resistance. Through the courtesy of Dr. Arzberger,[2] the writer had the opportunity to read an unpublished paper on some investigations regarding the causes of the nema resistance of several cowpeas. The results were that of five studied varieties, the more resistant, Iron and Brabham, had the roots best guarded by protective tissue; their cork layer was better developed and had fewer broken areas; the cork cells had more suberized walls, and the mechanical tissue in the cortex was, on the whole, more uniformly distributed. Furthermore, the cells containing starch were more remote from the periphery of the root, and starch was not so abundant as in the cortex of the non-resistant varieties. It will be one of the first tasks in coming investigations to define more clearly the causes of the restistance of plants as outlined above. It might then be difficult sometimes to distinguish true resistance from immunity. A number of similar cases are known, however, for insects (see 40, 48, 58, and others).

The Problem of Host Immunity

If we compare different nema-infested plant species, we notice that the degree in which they suffer from attacks is quite variable. One plant species will suffer much from a light attack and even be killed, whereas another species will show, in even a heavy grade of infestation, no signs of real suffering. In this connection one of the many examples in literature is cited. *Papaya gracilis* seems to suffer more and to react more differently from the attacks of *Heterodera radicicola* than numerous other plants.

[2] Arzberger, E. G. A comparative morphological study of cowpea roots resistant and non-resistant to nematode infestation. [Unpublished.]

According to Beille (5), the swellings here reach only the size of a hazel nut and then decay, whereas other plants, for example, *Dioscorea illustrata*, according to Queva (42), seems to be absolutely indifferent, in that infested specimens show no difference from the uninfested ones, and in some cases *H. radicicola* even seems to be useful to the host. This is stated by Vuillemin and Legrain (61) for a number of crop plants in the dry soils of the oases in the Sahara. These plants lignify the walls of the giant cells due to the attack of the parasite and use the so-formed cavities as water reservoirs. This makes them able to accumulate water for the hot part of the day and thus to withstand the dryness, while specimens not harboring *H. radicicola* perish. Here the parasitism is changed into a useful symbiosis. Here, again, is an entirely separate problem, that of host immunity. In the study of the nemic pests the phenomena of non-attraction, host indifference, host repellancy, and host resistance were all termed immunity, despite the fact that they are very different phenomena. The immunity problem involves the whole behavior of a plant actually under influence of the attacking nema. To separate this phase of the mutual relationship of plant and nema is not only an aid in allowing the investigator a much more precise outline of all questions to be studied, but is an actual progress in the knowledge of the matter itself.

In the study of this immunity problem, it is again the morphology of the nema which gives the basic facts and conceptions. Many plant infesting nemas possess relatively huge so-called salivary glands. On the other hand, botanists and other investigators with very little knowledge of a nemic organism claim that the plant attacked is under the influence of some secreta of the nema.

A third point is that the spear present in these parasitic nemas is said by some investigators (6) not to be a means for actual attack and puncturing of the plant cells, as first was thought. Observations show that this spear is only a trifle protruded, its action being a quickly repeated running back and forth so that the point hardly comes out of the mouth opening. Furthermore, the spear is often so narrow and fine that the conception of its being the direct means of the destruction and swallowing of plant cells and their contents must be dismissed. A study of attacked plant tissue also shows that no cells are emptied or destroyed in a mechanical way (38, pp. 151–173).

The action of the nema on the plant is apparently as follows: The nema ejects into the tissue of the plant by means of a short but rapid back-and-forth movement of its spear a liquid substance, presumably a secretion of the strongly developed salivary glands. Under the influence of this secretion the plant reacts in various ways, forming the giant cells (nectarial cells) (38) and tumor-like outgrowths, fluid exudates, etc. Perhaps also the excreta of the parasites living entirely inside the plant may contribute

stimuli to reactions, or at least influence the plant cells in their behavior. The so-called giant cells are formed only just around the mouth opening of the parasitic *Heterodera*, showing with evidence that they must be formed under the influence of an agent coming from the mouth opening. The careful examinations of the plant tissues showed no mechanical injuries to these cells, so apparently the spear itself is not the cause. What can it be therefore but the secretions from the huge salivary glands of which the outlet leads directly behind the spear into the oesophageal tube?

It seems to me, therefore, that there is much evidence that the harm these plant-parasitic nemas do to their host in the first degree is not mechanical, but toxic. The plant species, however, seem to react quite differently toward these toxins; and here is the point where the immunity problem begins. Have certain plants substances to bind, to neutralize these toxins? Are there antibodies present? We do not know, but future investigators will have to keep this problem in mind. It is not only of theoretical, but also of practical, interest. Might it not be that such knowledge could lead us to therapeutical treatments of nema-infested plants? If an annual crop plant is suffering under nemic infestations, there is at least this way to kill the plant and with it the harbored pest. But applied nematology has as its goal also the cure of perennial plants, such as fig trees, citrus, peaches, vines, etc., to which such radical killing methods can not easily be applied. To avoid large financial losses, it seems that only theropeutical methods might be possible, although plant therapeutics are today still a field hardly touched (16, 46, 7), but there is no reason for the conception that they are impossible. In the literature chiefly about *Heterodera schachtii* we find mentioned again and again that potassium has a very beneficial effect on plants (sugar beets) attacked by *Heterodera*. This point stands out so well that at first the reason for the bad growth of infested sugar beets was thought to be a scarcity of potassium in the soil. Today, the connection of potassium with a better growth of Heterodera-infested sugar beets has not been cleared. This connection is apparently not only a purely nutritive effect which the potassium has, but it also points toward a certain neutralization of the toxic influence of the parasites. If that is so, might it be possible in the future to step forward and find substances being fully parasitotrop (nematrop) and little, or not at all organotrop?

SUMMARY

1. The question is raised how the soil nemas, especially the plant-parasitic forms, locate their food, their host plants. A number of examples and observations are given which show the ability of the nemas,
   a. to distinguish their hosts at considerable distances and to locate them in an active way;

b. to distinguish between the different hosts and to choose the one they prefer.

2. But it is shown that the behavior of different populations of one plant-parasitic nema species toward the same host plant is variable, often showing gradual differences from heavy to light attacks, sometimes even to an imperceptible infestation.
3. It is shown that these differences in infestation of the same host plant by various populations of the same nema species are a result of conditions which lie within the nema and not within the plant, and that the situation is as follows:
   a. A plant-parasitic nema apparently prefers always the host species or even the host variety on which its parents lived; the host principle, as established by Hopkins for insects, is also applicable to our plant-parasitic nemas.
   b. This preference for a certain host grows with the number of generations a nema population lives on it, the latter getting more and more specialized on this very host. This specialization may reach such a high degree that finally even new hosts of the closest taxonomical, physiological, and chemical relationship to the old host are attacked no more or very lightly.
   c. In the judgment of the behavior of a nema population toward its host, the former host history is always of primary importance and in addition to this also, the possibility of choice. Forced by starvation, a nema population will attack a host which it will completely ignore if a more preferred one is present.
4. The mechanism of this host selection is outlined, based upon the observations and experiments of Buerkel, Baunacke, Rensch, and others, and a close study of the morphology of the sense organs of the involved plant-parasitic forms. It is shown that this mechanism works apparently as follows. The growing plants produce some root secretions which are carried by the soil water and act as stimuli upon the nemas The latter apparently perceive the stimuli with a sense organ called amphid or lateral organ which is thought to be a chemical sense organ. Presumably with the aid of these amphids the nema moves toward points of higher concentration of the stimulating fluid and so finally locates its host. The structure of the amphids of a few plant-parasitic nema species is for the first time described and their importance in general for the nemas discussed.
5. The dominating significance of the host selection mechanism, as outlined, is shown:
   a. in its power to explain fully the otherwise puzzling behavior of the nemas towards their hosts, a behavior which in the past resulted in so many seemingly contradictory observations.

b. in its practical importance for various control methods, such as Kühn's trap- or catch-plant method, Baunacke's "Reizpflanzen" method, Rensch's recently developed activation method of the cysts of the sugar beet nema, the crop-rotation method, and furthermore for all studies on host immunity, host resistance, host attraction, host indifference, and host repellancy.

c. in its theoretical significance for the conception of species, varieties, races, and strains of the nemas involved.

BUREAU OF PLANT INDUSTRY,
WASHINGTON, D. C.

LITERATURE CITED

1. ATKINSON, G. F. Nematode root-galls. Jour. Elisha Mitchell Sci. Soc. **6**: 81–130. 1889.
2. BASTIAN, H. C. Monograph on the anguillulidae, or free nematoids, marine, land, and fresh-water; with descriptions of 100 new species. Trans. Linn. Soc. London **25**: 73–184. 1865.
3. BAUNACKE, W. Untersuchungen zur Biologie und Bekämpfung des Rübennematoden *Heterodera schachtii* Schmidt. Arb. Biol. Reichsanst. Land. u. Forstw. **11**: 185–288. 1922.
4. BAYLIS, H. A. Some consideration on the host-distribution of parasitic nematodes. Jour. Linn. Soc. (London), Zool. (1923) **36**: 13–23. 1924.
5. BEILLE, L. Sur les altérations produites par l'*Hetérodera radicicola* sur les racines du *Papaya gracilis*. Assoc. Franc. Avancement Sci. Compt. Rend. Nantes (1898) **27**(2): 413–416. 1899.
6. BERLINER, E., and K. BUSCH. Über die Züchtung des Rübennematoden (*Heterodera schachtii* Schmidt) auf Agar. Biol. Centbl. **34**: 349–356. 1914.
7. BINZ, A., and H. BAUSCH. Versuch einer Chemotherapie des Gerstenbrandes. Ztschr. Angew. Chem. **35**: 241–243. 1922.
8. BRUMPT, E. Mode de pénétration des Nématodes dans l'organisme des Mammifères, Histotropisms et Histodiagnostic. Compt. Rend. Soc. Biol. (Paris) **85**: 203–206. 1921.
9. BUERKEL, E. Biologische Studien über die Fauna der Kieler Föhrde. 55. Kiel and Leipzig. 1900.
10. CAPUS, J., and P. MARCHAL. Sur la Maladie Vermiculaire des pois dans la Gironde. Compt. Rend. Acad. Agr. France **4**: 712–716. 1918.
11. CHANDLER, A. C. Speciation and host relationships of parasites. Parasitology **15**: 326–339. 1923.
12. COBB, N. A. Draconema: a remarkable genus of marine free-living nematodes. Jour. Wash. Acad. Sci. **3**: 145–149. 1913.
13. ———. Proceedings of the Helminthological Society of Washington. Jour. Par. **11**: 118–119. 1924.
14. CRAIGHEAD, F. C. Hopkins host-selection principles as related to certain Cerambycid beetles. Jour. Agr. Res. **22**: 189–220. 1921.
15. DAVIDSON, W. M. Alteration of hosts in economic aphids. Jour. Econ. Ent. **11**: 289–293. 1918.

16. DEMENTIEV, A. (DEMENTJEW, A.). Zur Frage der inneren Therapie der Pflanzen. Jour. Exp. Agron. Petrograd **15**: 282–293. (In Russian, German résumé, p. 292–293.) 1914.

17. EHRLICH, P. Die Grundlagen der experimentellen Chemotherapie. Ztschr. Angew. Chem. (1909) **23**: 2–8. 1909.

18. FILIPJEV, I. Zur Kenntnis des Nervensystems bei den freilbenden Nematoden. Trav. Soc. Imp. Nat. St. Petersbourg **43**: 205–215, 220–222. (In Russian, German résumé, p. 220–222). 1912.

19. FUCHS, C. Beiträge zur Biologie des Rübennematoden *Heterodera schachtii*. Ztschr. Landw. Versuchsw. Oesterr. **14**: 932–952. 1911.

20. FÜLLEBORN, F. Biologische Erwägungen über die Wanderung der Larven parasitischer Nematoden im Körper des Wirtes. Arch. Schiffs- u. Tropen Hyg. **27**: 444–452. 1923.

21. GOLDSCHMIDT, R. Histologische Untersuchungen an Nematoden. I. Die Sinnesorgane von *Ascaris lumbricoides* L. und *A. megalocephala* Cloqu. Zool. Jahrb., Abt. Anat. u. Ontog. Thiere **18**: 1–57. 1903.

22. GOODEY, T. On the susceptibility of clover and some other legumes to stem-diseases caused by the eelworm, *Tylenchus dipsaci*, Syn. *devastatrix*, Kühn. Jour. Agr. Sci. **12**: 20–30. 1922.

23. HAGMEIER, A. Beiträge zur Kenntnis der Mermithiden. Zool. Jahrb., Abt. System., Georg. u. Biol. Thiere **32**: 521–612. 1912.

24. HOLLRUNG, M. Das Auftreten der Rübennematode an Erbsen und andern Leguminosen. Deut. Landw. Presse **17**: 477. 1890.

25. ————————. Jahresbericht über die Tätigkeit der Versuchsstation für Nematodenvertilgung und Pflanzenschutz. 26 p. Halle. 1891.

26. HOPKINS, A. D. Economic investigations of the scolytid bark and timber beetles of North America. U. S. Dept. Agr. Program of work 1917: 353. 1916.

27. JOHNSON, G. E. On the nematodes of the common earthworm. Jour. Micros. Sci. **58**: 605–652. 1913.

28. KÜHN, J. Neuere Versuche zur Bekämpfung der Rübennematoden. Ztschr. Pflanzenkrank. **1**: 85–86. 1891.

29. LIEBSCHER, G. Über die Ursachen der Rübenmüdigkeit. Ztschr. Ver. Rübenzucker-Indus. **28**: 616–650. 1878.

30. ————————. Beobachtungen über das Auftreten eines Nematoden an Erbsen. Jour. Landw. **40**: 357–368. 1892.

31. LOOSS, A. The anatomy and life history of *Agchytostoma duodenale* Dub. Rec. Egypt. Govt. School Med. **3**: 5–158. 1905.

31a. ————————. The Sclerostomidae of horses and donkeys in Egypt. Rec. Egypt Govt. School Med. 1901.

32. MCCLINTOCK, J. A. Report on resistant plants for root-knot nematode control. Ga. Agr. Exp. Sta. Circ. **77**: 1–4. 1922.

33. MARCINOWSKI, K. Parasitische und semiparasitisch an Pflanzen lebende Nematoden. Arb. K. Biol. Anst. Landw. Forstw. **7**: 1–192. 1909.

34. MARTINI, E. Die Anatomie der *Oxyuris curvula*. Ztschr. Wiss. Zool. **116**: 137–534. 1916.

35. MÜLLER, H. C., and E. MOLZ. Versuche zur Bekämpfung des Rübennematoden *Heterodera schachtii*. Ztschr. Ver. Deut. Zuckerindus. (Tech. Thiel) (N. F. 51) **64**: 959–1050. 1914.

36. ————, ————. Versuche über den Einfluss der Vorfrucht auf den Nematodenbefall und den Ertrag der Zuckerrüben. Bl. Zuckerrübenbau **30**: 89–94. 1923.

37. NEAL, J. C. The root-knot disease of the peach, orange, and other plants in Florida, due to the work of Anguillula. U. S. Dept. Agr., Div. Ent. Bul. 20: 1–31. 1889.

38. NEMEC, B. Das Problem der Befruchtungsvorgänge und andere zytologische Fragen. 532 p. Berlin. 1910.

39. NILSSON-EHLE, H. Über Resistenz gegen *Heterodera schachtii* bei gewissen Gerstensorten ihre Vererbungsweise und Bedeutung für die Praxis. Hereditas **1**: 1–34. 1920.

40. OSHIMA, M. Formosan termites and methods of preventing their damage. Philippine Jour. Sci. **15**: 319–383. 1919.

41. POTTS, F. A. Notes on the free-living nematodes. Quart. Jour. Micros. Sci. (London). **55**: 433–484. 1910.

42. QUEVA, M. C. Modifications anatomiques provoquées par l'*Heterodera radicicola* Müll. dans les tubercules d'une Dioscorée. Assoc. France. Avancement Sci. Compt. Rend. Caen (1894) **23**(2): 629–633. 1895.

43. RAMSBOTTOM, J. K. Investigations on the narcissus disease. Experiments on the control of eelworm disease of narcissus. Jour. Roy. Hort. Soc. **43**: 51–64, 65–78. 1918.

44. RAUTHER, M. Beiträge zur Kenntnis von *Mermis albicans* v. Sieb. mit besonderer Berücksichtigung des Hautnerven-muskelsystems. Zool. Jahrb., Abt. Anat. u. Ontog. Thiere **23**: 1–76. 1906.

45. RENSCH, B. Eine neue Methode zur Bekämpfung der Rübennematoden. Mitt. Deut. Landw. Gesell. **39**: 412–414. 1924.

46. RIEHM, E. Zur Chemotherapie der Pflanzenkrankheiten. Ztschr. Angew. Chem. **36**: 3–4. 1923.

47. RITZEMA BOS, J. Les Nematodes parasites des plantes cultivées. VI^e^ Cong. Internat. Agr. Paris **2**: 306–312. 1900.

48. SHARPLES, A. The lacticiferous system of *Hevea brasiliensis* and its protective function. Ann. Bot. **32**: 247–251. 1918.

49. SLOGTEREN, E. VAN. Address to the members of the International Conference of Phytopathology and Economic Entomology, June 28th, 1923. 24 p. Lisse, Holland. 1923.

50. STEINER, G. Die von A. Monard gesammelten Nemotoden der Tiefenfauna des Neuenburgersees. Bul. Soc. Neuchateloise Sci. Nat. (1917–18) **43**: 142–240. 1919.

51. ————. Betrachtungen zur Frage des Verwandtschaftsverhältnisses der Rotatorien und Nematoden. Festschrift f. Zschokke **31**: 1–16. Basel. 1920.

52. ————. *Aplectana kraussëi* n. sp., eine in der Blattwespe *Lyda* sp. parasitierende Nematodenform, nebst Bemerkungen über das Seitenorgan der parasitischen Nematoden. Centbl. Bakt. (II) **59**: 14–18. 1923.

53. ————. A study on some nemas from the alimentary tract of the Carolina tree frog (*Hyla carolinensis* Pennant) with a discussion of some general problems of nematology. Jour. Par. **11**: 1–32. 1924.

54. ————. Contributions to the knowledge of some plant parasitic nemas and some related forms. Jour. Agr. Res. 28: 1059–1066. 1924.

55. STRASSEN, O. L. zur. Anthraconema, eine neue Gattung freilebender Nematoden. Zool. Jahrb. Sup. **7**: 301–346. 1904.

56. TISCHLER, G. Ueber Heterodera-gallen an den Wurzeln von *Circaea lutetiana* L. Ber. Deut. Bot. Gesell. (1901) 19 (Generalversammlungsheft): 95–107. 1902.

57. TRÄGARDH, I. On the chemotropism of insects and its significance for economic entomology. Bul. Ent. Research **4**: 113–117. 1913.

58. TREHERNE, R. C. The natural immunity or resistance of plants to insect attack. Agr. Gaz. Canada **4**: 855–859. 1917.

59. VOIGT. Beitrag zur Naturgeschichte des Rüben-Hafer- und Erbsennematoden (*Heterodera schachtii*). Deut. Landw. Presse 19: 813–815. 1892.

60. ———. Neue Varietät des Rübennematoden (*Heterodera schachtii*). Verhandl. Naturhist. Ver. Preuss. Rheinlande 51 (Sitzber.): 94–97. 1894.

61. VUILLEMIN, P., and E. LEGRAIN. Symbiose de l'*Heterodera radicicola* avec les plantes cultivées au Sahara. Compt. Rend. Acad. Sci. (Paris) **118**: 549–551. 1894.

62. WEBBER, H. J., and W. A. ORTON. Some diseases of the cowpea. II. A cowpea resistant to root-knot (*Heterodera radicicola*). U. S. Dept. Agr., Bur. Plant Indus. Bul. 17: 23–36. 1902.

63. WILFARTH, H. Der Einfluss der Züchtung auf Krankheiten und Gebrauchswerth der Rüben. Ztschr. Ver. Deut. Zuckerindus. (Tech. Theil) (N. F. 37) **50**: 673–678. 1900.

64. WIMMER, G. Kann man den Nematodenschaden durch Düngungsmassnahmen verringern? Deut. Zuckerindus. **31**: 18–21. 1906.

65. WOLLENWEBER, H. W. Tätigkeitsbericht Pathologisches Laboratorium 1920. Mitt. Biol. Reichsanst. Land u. Forstw. **21**: 246–266. 1921.

PRESENCE OF THE EUROPEAN BROWN-ROT FUNGUS IN AMERICA

WALTER N. EZEKIEL

WITH THREE FIGURES IN THE TEXT

The presence on the Pacific Coast of a Monilia disease differing from the common brown-rot was first recorded in 1915 by Jackson (6), who described a pear disease caused by an unidentified *Monilia*. This was studied by Posey (9, 10) who found it different from "*S. cinerea*" elsewhere in the country, and from *S. fructigena* from England. Barss has described the typical blossom and spur blight injury caused on stone fruits and some varieties of pears; and, chiefly on the basis of Posey's work, proposed for the fungus the name *Monilia oregonensis* Barss and Posey (2, 3). More recently Rudolph described the Monilia blossom blight of apricots, destructive in California, with extensive investigations and directions for its control (13).

In a more detailed paper (4) the writer has given the results on which was based the conclusion (7) that the widespread and destructive brown-rot *Sclerotinia* common in this country, to which the name *S. americana* (Wormald) Norton and Ezekiel[1] has been applied, is specifically distinct from *S. cinerea* (Bon.) Schröter of Europe. In the course of this work some cultures from California and Oregon have been of special interest. The California cultures studied were from rotten apricot (S 45), peach (S 46 and S 47) and cherry (S 49) sent by Mr. B. A. Rudolph during the summer of 1923. Prof. H. P. Barss kindly furnished a culture of the Oregon spur-blight *Monilia* (S 56). These were compared with a large population of other single-spore cultures, also collected in this country and now all assigned to *S. americana*, and with *S. cinerea* and *S. fructigena* cultures from England and Holland. Of the California and Oregon strains mentioned above, all except that on apricot were found to be the true *S. cinerea*.

[1] As Pollock (8), Roberts and Dunegan (12) and the writer (4, p. 89) have previously pointed out, the name *S. fructicola* (Winter) Rehm was the first to be applied to what were probably apothecia of *S. americana*. If means of distinguishing *S. americana* from *S. cinerea* by the apothecial characteristics should be worked out, we might then be able to identify the dried specimens of Winter (15) more definitely with *S. americana*, which would then properly be called *S. fructicola*. For the present, it seems preferable to use Wormald's name *americana*, which was published with the first description (16) that differentiated the American species from the earlier known European forms.

CHARACTERIZATION OF S. AMERICANA AND S. CINEREA[2]

It would be needless to mention here all the experiments previously described (4) in which consistent differences have been demonstrated between the range of varieties of *S. americana*, on the one hand, and *S. cinerea*[3] strains, from all the sources mentioned, on the other; but it may be of interest to outline the methods that have since been found most convenient for their differentiation. (The use of type cultures for comparison is an advantage in connection with the tests which follow but is not indispensable.)

Cultural Characteristics in Potato Dextrose Agar Slants at 15–25° C. Strains of *S. cinerea* grow slowly and the surface of the colony is characteristically smooth and buffy brown to Saccardo's umber (11) in color, though with some strains it may be partly or entirely white. Conidia are absent or produced only sparsely and never in definite pustules, visible macroscopically, in any of the strains yet studied by the writer. On the other hand, almost all strains of *S. americana* produce abundant conidia in definite (Tilleul buff) pustules. Absence of such pustules is not necessarily an indication that the culture is of *S. cinerea*, since the more uncommon varieties of *S. americana*, var. V and VI (4), produce few or no conidia under these conditions; however with the common varieties of *S. americana* abundant development of conidia affords ready recognition by this method.

Petri Dish Cultures on Potato Dextrose Agar. *S. americana* grows rapidly, filling the whole plate with a colony homogeneous except for numerous concentric circles of conidia, or in some varieties, of aerial hyphae. With *S. cinerea* growth extends much less rapidly, and is characterized by zonation and lobing as shown in fig. 1. Conidia if present are not borne in definite pustules as is invariably the case with *S. americana*, but scattered around so that the surface of the colony may be smooth and of the characteristic dull-colored, somewhat velvety, appearance.

Growth in Drop Cultures. Growth in standardized hanging drop cultures furnishes a number of criteria for identification. The results discussed below have been obtained under these conditions: potato dextrose decoction (potatoes 200 gm., dextrose 10 gm., per liter) was used as the nutrient; drops were made with a 5 mm. loop, seeded with 30–50 conidia, sealed on shallow depression slides and incubated at 25° C.

In 15 to 18 (perhaps best in 16) hours after inoculation, observations of typical *S. americana* sporelings show only the original germ tube, gener-

[2] It will be noted that the differences mentioned between these fungi include substantially all of those first observed by Wormald, except that of differential production of oxidizing enzymes, as they proved of diagnostic value, with the modifications noted, throughout the large population studied by the writer.

[3] In the present paper, discussion of *S. cinerea* applies primarily to the forma *pruni* of Wormald.

ally with no side branches, or if branched the branches are small and distinctly subordinate. Though there may be local irregularities in this germ tube it is straight in its general direction of growth. With *S. cinerea* on the contrary, total linear growth is less (100 to 300 μ, while *S. americana*

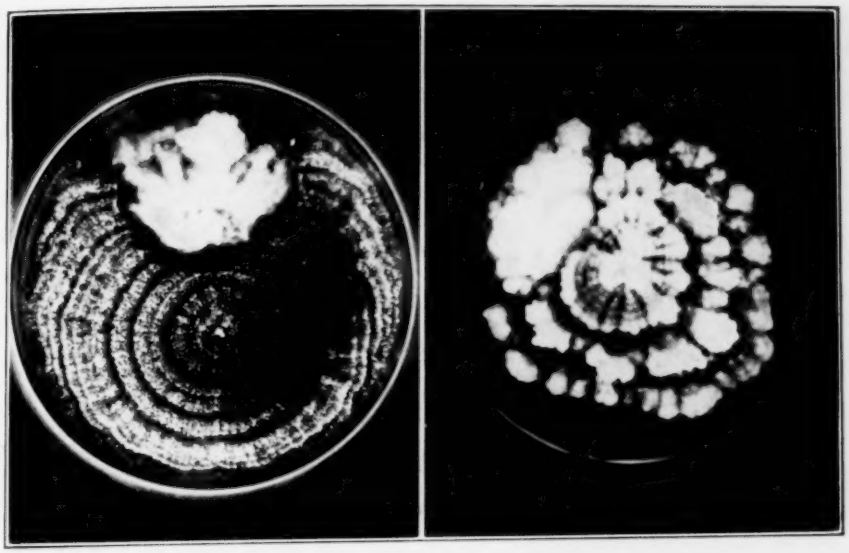

FIG. 1. Petri dish cultures on potato dextrose agar. Left, *S. cinerea* forma *pruni* (S 44) from England, upper colony and *S. americana* var. I (S 22) lower colony; inoculated at the same time at the same distance from the center. Grown 11 days, 13.5° C. Right, S 47, from California, one month at room temperature of about 15° C. [Direct prints (negatives) of the same cultures shown in regular photographs in Md. Bul. 271 (4), figs. 8 and 9.]

germ tubes are 500 to 1000 μ long), there may be three or four branches and the branches are characteristically of equal dimensions so that it is difficult or impossible, even in so young a colony, to pick out the original germ tube (fig. 2). Branching is almost invariably dichotomous, neither branch following the former direction of growth of the branching hypha so that a network of twisted, contorted, mycelium results.

Observations after three days yield equally definite differentiation. Fig. 3 shows the general appearance of the mycelium of *S. cinerea* and *americana*, which is itself distinctive. The *S. americana* hyphae are long and straight, and branching is simple—in glancing over the slide it is possible to pick out at once the older hyphae from which the branches arise. With *S. cinerea* the mycelium is of a much denser and more homogeneous nature. Each hypha arises from dichotomous branching. All twist and bend so frequently that it is unusual for a hypha to be found that is straight for even

the distance of a few fields of the microscope. This is markedly different from the *S. americana* hyphae, which can be traced straight, all the way across the drop.

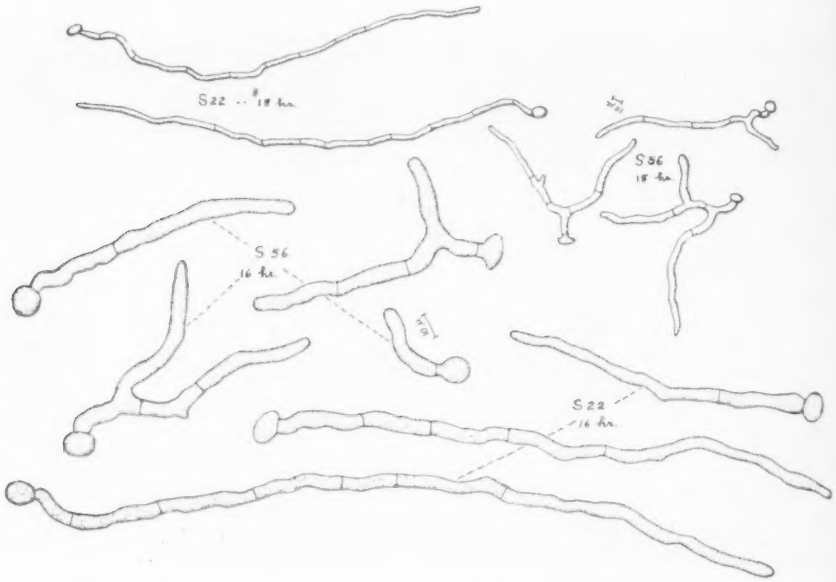

FIG. 2. Conidia of *S. americana* from Maryland (S 22) and *cinerea* from Oregon (S 56) germinating in drop cultures of potato dextrose decoction at 25° C. Note the characteristic geniculate branching in S 56. [Outlined with camera lucida.]

An additional distinction is the average length of the cells of the older hyphae. Growing under the standardized conditions mentioned, 19 sets of measurements, each including 25 cells of the larger hyphae of various strains of *S. americana* gave a mean value of 66 μ. A similar series of 10 sets of measurements of *S. cinerea* strains averaged only 36 μ.

In some recent series of drop cultures, with strains of previously well-established identity, atypical growth has at times been secured. Though this is unusual the fact that it has occurred indicates that the conditions specified for observation are not, as at first believed, sufficiently definite to allow us to consider the growth in single series of drop cultures, alone, the basis for differentiation. Until the method can be still more precisely worked out, perhaps with inorganic media, it would seem preferable to use it in connection with the cultural characteristics. In practice, microscopic identification in drop cultures has always agreed with the less laborious, macroscopic, cultural identification; and the former can doubtless be omitted except in doubtful cases.

IDENTITY OF THE PACIFIC SLOPE BLOSSOM BLIGHT MONILIA

The cultures from California and Oregon, mentioned before, fitted in with the *S. cinerea* cultures from Europe exactly, by these tests as well as in various inoculation experiments, spore measurements, etc. In drop cultures the results were identical. Their cultural characteristics on solid and liquid media, in tubes, agreed throughout. While constant individual differences could be seen in Petri dish cultures, the series as a whole agreed exactly with the series of strains of *S. cinerea* from Europe. Individual variation noted was hardly of a greater degree than that previously described between cultural varieties of *Sclerotinia americana*. Accordingly, it seems proper to designate these Pacific Coast cultures as *Sclerotinia cinerea*.

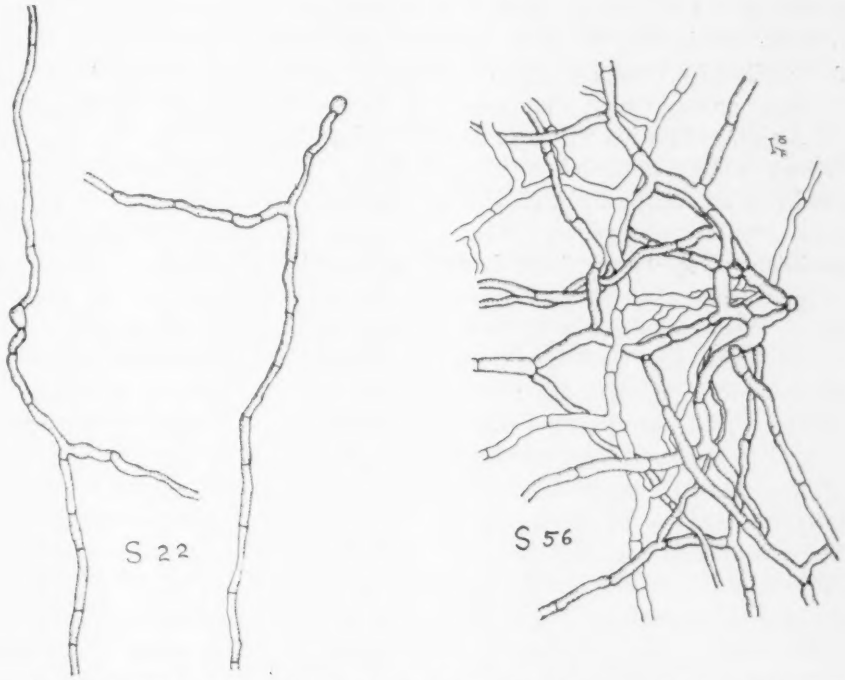

FIG. 3. General mycelial characteristics in two-day old drop cultures of *S. americana* (S 22) and *S. cinerea* (S 56). Growth is more extensive with *S. americana* but very loose, while with *S. cinerea* a great amount of branching occurs though the entire colony is small. [Outlined with camera lucida.]

This conclusion is of especial interest in connection with the Oregon fungus. This culture was supplied by Prof. Barss, who has recently discussed the life history of this organism and considered it distinct from all described species. Though as shown also by the studies above the organism

is quite different from *S. americana*, it resembles rather clearly the earlier-known *S. cinerea* of Europe; and the life history which Barss cites to differentiate his *M. oregonensis* from the ordinary brown-rot fungus is a further resemblance to *S. cinerea;*

(1) The apothecial stage of *S. cinerea* has been authentically found only by Wormald (17), unless the *S. laxa* of Aderhold and Ruhland (1) or the *Sclerotinia* on cherries of Westerdijk (14) can be assigned to that species. Similarly, Barss reports that the Oregon fungus failed to produce apothecia under experimental conditions resulting in abundant development of *S. americana* apothecia.

(2) While the Oregon *Monilia* produces conidia much like those of *S. americana*, they develop much more sparingly in culture, and on twigs and flower parts are produced mainly, not during the summer following infection, but late in winter or early the following spring. Here again, *S. cinerea* is described by Wormald (18) as producing pustules of conidia on the bark of shoots or cankers on plum trees only from about December to February.

A similar relation was developed experimentally by the writer in inoculations on fruits in the laboratory (4, p. 119). Generally strains of *S. cinerea* produced no conidia while those of *S. americana* produced amounts varying with the different strains; but in an extensive series on Shockley apples no conidia developed away from the point of inoculation with any *S. americana* strains, while pustules were produced on most of the *S. cinerea* inoculations, which included two of the California strains (S 47 and S 49).

(3) The Oregon fungus is found more frequently on blossoms and twigs and causes "a negligible amount of fruit rot." This is not unlike *S. cinerea* which has attracted much more attention in Europe as a parasite of the woody part of the tree than *S. americana* has in this country. It is perhaps hardly remarkable that little infection on fruit occurs when one considers that the organism generally produces conidia before blooming and not after fruit are developed. Moreover, the slow rate of growth of *S. cinerea* in infected fruits, as compared with that of *S. americana*, coupled with the absence or scarcity of conidia on them during the summer, might tend to lessen the chance of such specimens being collected and studied. (This last point has come up in connection with our survey of the Maryland brown-rot diseases.)

(4) Barss considers artificial cultures of the Oregon fungus different from those of any described species. This is of course true in the sense that each isolation of the brown-rot fungi results in a strain of unique cultural characteristics, and distinguishable by sufficient study from any other strain. However in the cultures studied by the writer, S 56 from Oregon resembled much more closely a culture received from Wormald, S 44, than

the latter did S 47 from California, a strain agreeing exactly with Wormald's description of *S. cinerea* cultures.

PATHOLOGICAL SIGNIFICANCE OF THE PRESENCE OF S. CINEREA IN AMERICA

Diseases due to what is probably *S. cinerea* have been studied in Oregon (2) and California (13) where the predominant *S. americana* is also present. Barss, who distinguishes between the two organisms, attributes greater injury in the form of blossom and twig blight to the *S. cinerea*, but finds it of less economic importance because it causes little injury in the form of fruit rot as compared to *S. americana*. On the other hand, *S. cinerea* is found to attack not only stone fruits but also some varieties of pears.

SUMMARY

1. Isolations from fruits from California, and the spur blight *Monilia* from Oregon, were identified as the true European brown-rot fungus, *Sclerotinia cinerea* (Bon.) Schröter.

2. Methods are outlined by which *S. cinerea* can be distinguished, by cultural characteristics as well as microscopically by numerous mycelial characters in drop cultures, from *S. americana*, the species occurring predominantly in this country.

3. *Monilia oregonensis* Barss and Posey agrees morphologically, culturally and in its life history with *S. cinerea*, and is doubtless to be considered synonymous.

4. *S. cinerea* causes blossom and twig blight injury, with little fruit rot, to a wide range of hosts. It has not been considered so destructive as *S. americana* in reports from regions where both occur.

AGRICULTURAL EXPERIMENT STATION,
UNIVERSITY OF MARYLAND.

LITERATURE CITED

1. ADERHOLD, R. and W. RUHLAND. Zur Kenntnis der Obstbaum-Skerotinien. Arb. Biol. Abt. Land-u. Fortw. Kais. Ges. **4**: 427–442. 1905.
2. BARSS, H. P. Brown-rot and related diseases of stone fruits in Oregon. Ore. Agr. Exp. Sta. Circ. **53**: 3–18. 1923.
3. ————. Serious blossom blight in Pacific Northwest orchards due to a species of Monilia. (Abst.) Phytopath. **15**: 126. 1925.
4. EZEKIEL, WALTER N. Fruit-rotting Sclerotinias II. The American brown-rot fungi. Md. Agr. Exp. Sta. Bul. **271**: 87–142. 1924.
5. ————. Presence of the European brown-rot fungus in America. (Abst.) Phytopath. **15**: 55, 1925.
6. JACKSON, H. S. Pear canker, *Monilia* sp. Ore. Agr. Exp. Sta. Bien. Crop Pest and Hort. Rpt. (1913–14) **2**: 271–272. 1915.
7. NORTON, J. B. S. and WALTER N. EZEKIEL. The name of the American brown-rot *Sclerotinia*. (Abst.) Phytopath. **14**: 31–32. 1924.

8. POLLOCK, J. B. *Sclerotinia fructigena* in Europe and America. Mich. Acad. Sci. Rpt. **11**: 49–53. 1909.
9. POSEY, G. B. Studies of *Monilia* blight of fruit trees. Sci. **42**: 583. 1915.
10. ————. Studies of *Monilia* blight of fruit trees. (Abst.) Phytopath. **5**: 294. 1915.
11. RIDGWAY, ROBERT. Color standards and color nomenclature. *43 p.*, illustrated. Washington, D. C. 1912.
12. ROBERTS, JOHN W. and JOHN C. DUNEGAN. The fungus causing the common brown rot of fruits in America. Jour. Agr. Res. **28**: 955–960. 1924.
13. RUDOLPH, B. A. *Monilia* blossom blight (brown rot) of apricots. Calif. Agr. Exp. Sta. Bul. **383**: 3–55. 1925.
14. WESTERDIJK, JOHANNA. Die *Sclerotinia* der Kirsche. Med. phytopath. Lab. "Willie Commelin Scholten" **3**: 39–41. 1912.
15. WINTER, GEORG. Uber einige nordamerikanische Pilze. II. Hedwigia **22**: 131. 1883.
16. WORMALD, H. The "brown rot" diseases of fruit trees with special reference to two biologic forms of *Monilia cinerea*, Bon. I. Ann. Bot. **33**: 361–404. 1919. II. Ann. Bot. **34**: 143–171. 1920.
17. ————. On the occurrence in Britain of the ascigerous stage of a "brown rot" fungus. Ann. Bot. **35**: 125–135. 1921.
18. ————. Further studies of the "brown rot" fungi. I. A shoot-wilt and canker of plum trees caused by *Sclerotinia cinerea*. Ann. Bot. **36**: 305–320. 1922.

STUDIES ON THE MOSAIC DISEASE OF NICOTIANA GLUTINOSA

M. N. WALKER[1]

WITH PLATE XXIV

INTRODUCTION

A great amount of cross-inoculation work during the past few years has pointed to a common casual agency for many of the mosaic diseases, and the apparent existence of two distinct mosaic diseases within the single genus *Nicotiana* led the writer to the further investigation which this paper reports.

LITERATURE

The literature of direct bearing on the question consists of two papers by Allard. The first paper appeared in 1916 (2), giving data which indicated that a mosaic disease on *N. viscosum* was distinct from that on tobacco, *N. tabacum* L. A later paper which appeared in 1917 (4) merely mentioned the existence of a mosaic disease on *N glutinosa L.*, which was distinct from that on tobacco. The similarity in literal meanings of the specific names of these two species of *Nicotiana*, said to bear mosaic diseases distinct from tobacco mosaic, led the writer to inquire of Dr. Allard whether the species were identical. Dr. Allard explained that through error the term *Nicotiana viscosum* had been used in place of *Nicotiana glutinosa*, and that the correct name had been substituted in the second paper. Dr. Allard also stated that he had at no time worked on *N. viscosum*, and kindly enclosed a description of the two distinct species which follows. In this description *N. viscosa* is substituted for *N. viscosum* as a preferred spelling.

"*Nicotiana glutinosa* L. Leaves long petioled, cordate, entire, villous-pubescent. Flowering racemes secund or one-sided. Calyx more or less bilabiate. Lowermost usually bifid, the uppermost trifid. Corolla sub-ringent, twice as big as the calyx. Stamens unequal, tomentose at the base.

"*Nicotiana viscosa*. Stems viscid-villous, erect, angulate branched. Branches axillary, short, with flowers at the apex. Leaves serrate, entire, repand; lowermost and middle cauline somewhat wedge-shaped, obtuse, narrowed toward the base then becoming dilated and half clasping. Racemes sub-corymbose terminating the stem and branched. Calyx lobes unequal, short, obtuse. Corolla funnel-form, tube cylindrical slightly enlarged, about twice as long as the densely hairy calyx. Leaves average only two or three inches long by two-thirds inch in width."

[1] The writer is indebted to Dr. S. P. Doolittle, of the Office of Cotton, Truck, and Forage Crop Disease Investigations, for suggestions and advice during the progress of this work.

The plants used in the writer's experiments agree perfectly with the description of *N. glutinosa* (Pl. XXIV, A).

DESCRIPTION OF THE SYMPTOMS OF THE MOSAIC DISEASE OF NICOTIANA GLUTINOSA

Possibly on account of the less succulent nature of *N. glutinosa*, the symptoms of the mosaic disease of this species are less striking than those appearing on the more succulent leaves of tobacco. In early stages of the disease, the tipmost leaves assume a faintly mottled appearance, sometimes so faint as to be scarcely discernible. These early symptoms may gradually become more intense until a decidedly mottled, dwarfed, and malformed plant (Pl. XXIV, B and C) may result, or they may gradually fade until the plant shows only the faintest possible traces of mottling. It has been found that when inoculations are made during favorable weather conditions, the average incubation period is about ten days.

RESULTS OF CROSS-INOCULATIONS FROM MOSAIC TOBACCO TO N. GLUTINOSA

In these experiments, all inoculations were made by inserting crushed leaf tissue from mosaic tobacco plants into stems and leaves of healthy young plants of *N. glutinosa*. On account of the stickiness of the leaves of *N. glutinosa* it was impossible to use aphids as a means of inoculation.

The *N. glutinosa* seedlings used for inoculation were all healthy and showed no signs of mosaic infection up to the time of inoculation, when they were in the four or five-leaf stage. As there were no mosaic *N. glutinosa* plants in the greenhouses during the original inoculations, the infection of the young *N. glutinosa* plants undoubtedly resulted from the inoculations. This fact was made even more certain by the fact that during three years of observation in the greenhouses no insects have ever been known to attack plants of this species.

The results of these inoculations are shown in table 1.

RESULTS OF CROSS-INOCULATIONS FROM MOSAIC PLANTS OF N. GLUTINOSA TO TOBACCO

The fact that tobacco plants are susceptible to the mosaic disease of *N. glutinosa*, as shown in table 2, further indicates the probability that the mosaic diseases of these two hosts are identical. Time did not allow the carrying out of a very extensive series of inoculations from *N. glutinosa* to other plants, but a few small experiments furnished the following results. Two tomato plants out of eight became infected when inoculated with crushed leaf tissue from mosaic *N. glutinosa* plants. Infection also was obtained in a small number of inoculations from mosaic plants of the cultivated ground-cherry to healthy young *N. glutinosa* plants.

TABLE 1.—*Results of inoculations from mosaic tobacco to Nicotiana glutinosa*

Date inoc.	Source of inoculum	No. plants inoc.	No. plants mosaic	Date of observation
5/30/23	Crushed leaf tissue from mosaic tobacco	6	6	6/11/23
5/30/23	Crushed leaf tissue from healthy tobacco (Control)	6	0	6/11/23
7/24/23	Crushed leaf tissue from mosaic tobacco	16	8	8/ 6 /23
7/24/23	Crushed leaf tissue from healthy tobacco (Control)	16	0	8/ 6 /23
7/25/23	Crushed leaf tissue from mosaic tobacco	16	8	8/ 6 /23
7/25/23	Crushed leaf tissue from healthy tobacco (Control)	16	0	8/ 6 /23
8/ 6 /23	Crushed leaf tissue from mosaic tobacco	25	11	8/28/23
8/ 6 /23	Crushed leaf tissue from healthy tobacco (Control)	20	0	8/28/23
4/29/24	Crushed leaf tissue from mosaic tobacco	16	2	5/19/24
4/29/24	Crushed leaf tissue from healthy tobacco (Control)	16	0	5/19/24

TABLE 2.—*Results of inoculations from mosaic N. glutinosa to tobacco*

Date inoc.	Source of inoculum	No. plants inoc.	No. plants mosaic	Date of observation
6/14/23	Crushed leaf tissue from mosaic *N. glutinosa*	12	2	7/ 2 /23
6/14/23	Crushed leaf tissue from healthy *N. glutinosa* (Control)	12	0	7/ 2 /23
2/28/24	Crushed leaf tissue from mosaic *N. glutinosa*	40	5	3/15/24
2/28/24	Crushed leaf tissue from healthy *N. glutinosa* (Control)	24	0	3/15/24
2/28/24	Crushed leaf tissue from mosaic *N. glutinosa*	6	2	3/15/24
5/20/24	Crushed leaf tissue from mosaic *N. glutinosa*	9	3	6/ 6 /24

DISCUSSION

In the course of this work it was found that during midwinter *N. glutinosa* plants did not show the decided symptoms which appeared during the spring months, and, in fact, several series of inoculations made during midwinter were discarded by the writer on account of the doubtful nature of the symptoms. Some of these plants when set aside, however, developed definite mosaic symptoms several weeks later. A thing of this sort has probably occurred in other plants, for some mosaic diseases have been reported to have a much longer incubation period than that later accepted, as workers by longer acquaintance with the disease were able to diagnose the fainter symptoms. This failure to produce symptoms during midwinter was probably due to a condition of the host which prevented the manifestation of decided and recognizable symptoms, as the short and often cloudy days of midwinter retard the growth of plants to a decided extent. These points have been suggested in connection with plants other than *N. glutinosa*, as for example, *N. glauca* (1, 3), *Datura stramonium* (2), tomato (4, 7), petunia (3), physalis (8), *Phytolacca decandra* (6), and various *Nicotiana* species (5).

Nicotiana glauca presents a case analogous to the one in hand. Owing to the very faint manifestation of symptoms, it was at first thought that this plant was immune to tobacco mosaic, but it was later shown that it is susceptible (3). The experiments with this species were identical with those first described in connection with *N. glutinosa*.

In view of the observations on the failure of *N. glutinosa* to show symptoms following inoculation with tobacco mosaic in midwinter, and the fact that Allard's tabulated experiments were made between December 16, 1915, and January 29, 1916, the writer is inclined to believe that the data advanced by Allard does not necessarily conflict with the present work, and to believe that the mosaic diseases of tobacco and *N. glutinosa* are probably identical.

SUMMARY

1. The Nicotiana species called by Allard *Nicotiana viscosum* is properly called *Nicotiana glutinosa*.

2. The mosaic disease on tobacco is transmissible to *N. glutinosa* and the mosaic disease on *N. glutinosa* is also transmissible to tobacco.

3. Tomatoes are susceptible to the mosaic disease on *N. glutinosa*.

4. *N. glutinosa* may be infected with the mosaic disease on *Physalis pubescens*.

OFFICE OF COTTON, TRUCK, AND FORAGE CROP DISEASE INVESTIGATIONS,
BUREAU OF PLANT INDUSTRY,
WASHINGTON, D. C.

1. ALLARD, H. A. The mosaic disease of tobacco. U. S. Dept. Agr. Bul. 40: 1–33. 1914.
2. ————. A specific mosaic disease in *Nicotiana viscosum* distinct from the mosaic disease of tobacco. Jour. Agr. Res. **7**: 481–486. 1916.
3. ————. The mosaic disease of tomatoes and petunias. Phytopath. **6**: 328–335. 1916.
4. ————. Further studies of the mosaic disease of tobacco. Jour. Agr. Res. **10**: 615–631. 1917.
5. CLINTON, G. P. Chlorosis of plants with special reference to calico of tobacco. Conn. Agr. Exp. Sta. Ann. Rpt. **1914**: 357–424. 1914.
6. DOOLITTLE, S. P., and M. N. WALKER. Further studies on the overwintering and dissemination of cucumber mosaic. Jour. Agr. Res. [In press.]
7. GARDNER, M. W., and J. B. KENDRICK. Tomato mosaic. Purdue Agr. Exp. Sta. Bul. 261: 1–24. 1922.
8. WALKER, M. N. The relation of certain species of *Physalis* to the overwintering of cucumber mosaic. [In preparation.]

EXPLANATION OF PLATE XXIV

A. Healthy plant of *Nicotiana glutinosa*.
B. A mosaic *N. glutinosa* plant showing dwarfing and mottling. This plant also shows the fading out of symptoms. It will be noticed that the tip leaves are less mottled than some of the older leaves, a reversal of usual conditions.
C. A mosaic *N. glutinosa* plant showing dwarfing and malformation.

UNIV. OF MICH.

B
C
A

UNIV. OF MICH.

AN EFFECT OF DROUGHT IN THE FORESTS OF THE SIERRA NEVADA

E. P. MEINECKE

WITH TWO FIGURES IN THE TEXT

In the month of September, 1924, an alarming loss in seed trees left on a large timber-sale area was reported from the Stanislaus National Forest, California. Trees standing in groups scattered over the area were first observed to turn color in the beginning of September and within a very short time were unmistakably dying.

The area was visited and examined in the second half of September. The timber-sales area is located in the main on the north side of a sharp ridge sloping steeply into the Middle Fork of the Stanislaus River, at elevations between 4,000 and 6,000 feet. The forest type on the dry slopes is the usual one characterizing the granite hogbacks branching off east-west from the main backbone of the Sierra Nevada. Western yellow pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense cedar (*Libocedrus decurrens*) with some Douglas fir (*Pseudotsuga taxifolia*) are the chief components of the association in which scattered California black oak (*Quercus californica*) occupies a subordinate position. Climatologically the region is characterized by cold winters with heavy rain and snow, and hot, dry summers during which all vegetation depends for its water requirements on the supply stored and moving in the soil, without replenishment by summer rains.

It is apparent at first glance that the dying goes far beyond what could be classed as normal loss. All classes, from young trees of small pole-size up to larger individuals, are involved, including in one case a sugar pine of 45 inches D. B. H. Typically the trees die in groups of from 4 to 8 and 10 trees. The direct loss in timber values is considerable and the silvicultural effect on the remaining stand is in many places decidedly detrimental. Bare places are enlarged and the objects of marking are frequently thwarted by the breaking up of the groups left.

The dying is not confined to the cut-over land but also occurs in the virgin forest. Although it is decidedly commonest on the timber-sales area in question, groups of dying and dead trees were seen two miles from the nearest cutting and a few scattered groups were observed at greater distances.

The most striking characteristics of the killing are that the trees die from the top down and from the outside in, and that they die in groups,

often composed of two or more of the following species: yellow pine, sugar pine, white fir, and even black oak. The trees take on a fading dirty-green color which later tends to become reddish, and the needles look dry and wilted. The groups with their grey and discolored crowns stand out strongly against their vividly green surroundings. It is to be noted that none of the incense cedars associated with the dying trees of the other species showed any signs of distress. Several yellow pines, sugar pines, and white firs, but none of the oaks, were felled and partly peeled off for the purpose of examination.

In all the trees, with exception of the oaks, insects were plentiful at the time of cutting. Insects taken from these trees and later examined by the Office of Forest Insect Investigations were found to be species that would not be expected to cause the simultaneous dying of trees of different species and sizes in well defined groups.

The whole aspect of the trees pointed to the probability that the seat of the trouble lies in the lowest part of the bole or in the root system. Digging and exposure of the root system for examination was not feasible on account of the large size of the trees. No sign of any fungus which could have brought about the dying was found. The probabilities, however, speak rather against root fungi being at the bottom of the trouble. Both *Fomes annosus* and *Armillaria mellea* (or *Pholiota aurivella*) are known to spread from one tree to another, but it is not likely that all the trees of different species composing the group should die at the same time. It is also little probable that these fungi should cause the simultaneous death of trees differing so considerably in age and size.

Lightning, as one of the known causes of group-dying, can well be excluded from the discussion. The area affected has been remarkably free from lightning during the last two years, as far as can be ascertained, and any serious consequence of lightning shock in previous years must surely have become apparent within this period. Lightning frequently affects tree groups irrespective of species, and incense cedar would have suffered as much as the other species from a shock severe enough to cause death.

All the trees examined show that the annual ring of 1924 had stopped its growth relatively early in the season, while their sound neighbors had completed their growth. Only part of the spring wood is formed and the summer wood, which at the time of the examination should have been completed, is entirely lacking. Generally the ring has attained not more than one-fourth of the width of the 1923 ring, which latter is not below normal in spite of the drought prevailing in that year. As far as it is permissible to guess, the 1924 increment stopped some time in June or July. It is not probable that the insects now present were at work then and that the killing showed up two months later.

All indications point to the influence of a primary agency of a physical nature affecting the whole forest but becoming injurious only in conjunction with unfavorable local conditions. Under this assumption, neither the primary agency nor the adverse local conditions alone are sufficiently harmful to bring the trees to the point of death. When they combine, their effect may prove fatal.

The unprecedented drought prevailing in 1924 must have made itself felt in the life of the forest. The normal seasonal precipitation for California is 25.43 inches. The average for 1923–24 was only 12.18 inches or less than half the normal. The corresponding figures for the nearest Weather Bureau Station, Lake Eleanor, situated 30 miles south at a little lower elevation, are 39.2 inches, based on a 13-year record, and 20.83 inches, or a little more than half the average. As a consequence of this severe drought condition, the annual elimination of older foliage, which normally takes place in the fall, began this year in June and in some cases even earlier. The deficiency in soil water was undoubtedly least felt in bottom land and in close proximity to streams, and became more and more pronounced on steeper slopes and ridges. It must have been most marked where bed rock comes close to the surface and where trees live in pockets formed by the bed rock or by large boulders. As the trees grow their roots fill out the pockets as potted plants will fill out a flower pot. They finally become root-bound, and, while in normal years this condition may simply express itself in a toning-down of growth, it becomes fatal under excessively severe drought conditions. The trees had already gone through a drought in 1923, and the deficiency in precipitation during the winter of 1923–24 accentuated whatever physiological harm had resulted from it. The ground water, instead of being brought back to normal, receded to still greater depths. An excavation on the area of the timber sale in September of 1924 showed that the soil was dust dry to a depth of more than 13 feet, so that even in deep soils the majority of the trees must have suffered from a lack of water. In shallow soil pockets the supply is likely to be cut off entirely. When a number of trees stand together in the same pocket the effect must be cumulatively severe. None of the groups observed are located in bottom land or close to running water. In many cases they appear on slopes or benches where rock outcrops are common. In others no surface indication of rock is apparent, but the rights-of-way of the nearby logging railroad reveal that the distribution of soil and rock is often of the nature described.

Figure 1 shows the root system of a yellow pine of about 36 inches D.B.H. The tree had stood on the right-of-way and the stump had been pulled and removed. Instead of spreading freely through the soil the roots are closely compacted into an irregular cube of the shape of the narrow

—*Photograph by L. S. Gill*

FIG. 1. Yellow pine stump with root system, root-bound by confined growth in granite pocket.

pocket in which they grew. Figure 2 illustrates in detail the abnormal flattening of the roots against the granite walls of the pocket.

It is impossible to ascertain whether the particular tree shown in the figures had been dead when cut or would have succumbed later in the year. On one side only, a few roots have been able to escape out of the pocket into better soil and to provide the tree with a modicum of water. At any rate, the peculiar conformation of its root system may with propriety be used in the interpretation of the facts reported.

Rock pockets completely isolated from soil connected through capillarity with the deeper moister strata must be relatively rare. The attempted explanation of the phenomenon would account for the fact that the trees are dying in widely scattered groups, that the groups are composed of different species, and that death occurred at about the same time. While trees with normal root systems survived the drought with little injury and adjusted their water budget by prematurely eliminating surplus foliage, the abnormal drop in the water table made it increasingly difficult, and finally im-

—*Photograph by L. S. Gill*

FIG. 2. Same as Fig. 1. Detail of closely intertwining and rock-flattened roots.

possible, for pot-bound and isolated individuals or groups of trees to secure even the absolute minimum of moisture needed to maintain life.

The survival of incense cedar under conditions apparently identical with those which proved fatal to the other species remains unexplained. It may be that incense cedar adapts itself to adverse conditions, in particular to drought, even to a greater extent than has already been known.

The explanation attempted rests frankly upon surmise, supported by observational evidence. The handling of the root systems of timber ranging up to 40 and 50 inches D. B. H. and the excavation of huge granite pockets make detailed examinations prohibitive. Further observations along railroad rights-of-way and roads in the forest may furnish additional support for the view advanced.

OFFICE OF INVESTIGATIONS IN FOREST PATHOLOGY,
BUREAU OF PLANT INDUSTRY,
SAN FRANCISCO, CALIF.

PHYSIOLOGICAL EVIDENCE ON THE GENETIC IDENTITY OF NATURAL AND SYNTHETIC STRAINS OF WILD EMMER[1]

OLAF S. AAMODT AND MOSES N. LEVINE

Love and Craig (12), while engaged in the study of the genetics of F_2 segregates of a cross between *Triticum vulgare* Vil. var. Early Red Chief, and *T. durum* Desf. var. Marouani in 1918, observed types which closely resembled the wild emmer or so-called "wild wheat" of Palestine, *T. dicoccum dicoccoides* Kcke., which had been rediscovered by Aaronsohn (2) in 1906. The appearance of the wild form in the progeny of a cross between common and durum varieties is of profound interest, because it suggests the possible origin of the prototype of the common wheats.

Experiments were made by Love and Craig to determine how the characters of the natural wild emmer were inherited when crossed with other types. They found that " . . . the characters of the wild wheat behave in hybridization much as do the characters of the other wheat types" (12, p. 62). Further intensive inheritance studies by these authors (13) and careful cytological investigations[2] have confirmed the striking similarity between the natural wild emmer found by Aaronsohn and the synthetic wild type produced by Love and Craig.

A third method of studying the similarities of the two wild-emmer forms has suggested itself, namely, their reaction toward physiologic forms of stem rust (*Puccinia graminis* Pers.). That parasitic organisms might serve as adequate physiologic reagents in the determination of the phylogenetic relationship and taxonomic position of certain plant and animal hosts has been known since the days of Darwin. The literature dealing with this subject has been reviewed by Vavilov (19, 20) and Dufrénoy (4). In the present case it will suffice to cite the instances where fungous parasites have been successfully used as physiologic reagents.

As long ago as 1895, Eriksson (5) found that a certain wheat-rye hybrid was immune from the brown leaf rust of rye, *Puccinia dispersa* Erikss., and

[1] The writers are indebted to H. H. Love, Professor of Plant Breeding, New York State College of Agriculture, Cornell University, for supplying them with the seed material of the natural and synthetic wild emmers. They wish to express their grateful appreciation also to E. C. Stakman, Head of the Section of Plant Pathology, Minnesota Agricultural Experiment Station, and Pathologist, Office of Cereal Investigations, U. S. Department of Agriculture, for valuable suggestions and helpful criticisms.

[2] The cytologic studies were made by Ernest Dorsey, of Cornell University, and the results are being reported in a separate paper.

susceptible to the orange leaf rust of wheat, *Puccinia triticina* Erikss., which seemed to indicate that this hybrid was more closely related to the wheat than to the rye parent.

Klebahn (9, p. 140-141) mentions a case in which he discovered an error in the determination of a willow plant by inoculating it with a narrow specialized rust fungus, *Melampsora ribesii purpureae* Kleb.

Vavilov (18, 19, 20) used highly specialized, obligate parasites, such as *Erysiphe graminis tritici* March., *Puccinia triticina* Erikss., *P. graminis avenae* Erikss. and Henn., and *P. coronifera* Kleb., in an extensive genetic and systematic study of many varieties of wheat and oats. By the use of this method he succeeded in separating many varieties of these cereals into distinct races. The results were corroborated by the simultaneous use of other methods: hybridization, serum reactions, and cytologic examinations.

The effective application of parasitic organisms as physiologic reagents led Vavilov (20, p. 235) to the conclusion that, "this method can sometimes be very useful to genetists as well as to systematists, even for practical purposes of plant-breeding, especialy in giving useful suggestions, as to the possibility of crossing some species and varieties which morphologically may be quite distinct. For phylogenetical purposes this method can be used in the same way as hybridization, serum reactions, cytology, etc."

Stakman and Levine[3] were able to separate *Festuca elatior* Linn. from *F. pratensis* Huds., although the two grasses are considered as identical by some authorities, by the difference in their reactions to a strain of *Puccinia graminis phleipratensis* (Erikss. and Henn.) Stak. and Piem. *F. elatior* was absolutely immune from this rust, whereas *F. pratensis* was completely susceptible. Likewise they could distinguish *Agropyron repens* (L.) Beauv. from *A. tenerum* Vasey by their reaction to *P. graminis tritici* Erikss. and Henn.

Dufrénoy's (4) essay, based on the researches of Stakman and his coworkers (15, 11, 16), Chapman (3), Legrand (10), and others, points out that living organisms are the most delicate reagents of which we now have any knowledge or control. Dufrénoy, furthermore, brings out the fact that parasitic organisms can render evident those biochemic and biologic characters which are peculiar to each group of individuals and which are otherwise indiscernible.

Johnston and Bower (8) found that certain physiologic forms of *Puccinia graminis tritici* furnished them by the Minnesota laboratary could be used as an effective and rapid method in determining the purity of Kanred seed wheat. This method proved a valuable supplement to field inspection.

It has been demonstrated by Stakman and Levine (17) that several varieties of wheat show different degrees of resistance when inoculated with

[3] Unpublished results obtained by E. C. Stakman and M. N. Levine in 1915.

certain physiologic forms of *Puccinia graminis tritici*. These differences are consistent and constant and have been shown by various investigators (14, 6, 1, 7) to be definitely inherited genetic characters.

EXPERIMENTAL DATA

It was thought that a comparative study of the reaction of the natural wild and synthetic wild emmers to several physiologic forms of *Puccinia graminis tritici* might yield valuable information regrading the physiological similarities of these strains of wheat.

Five distinct physiologic forms were selected for the experiment: *Puccinia graminis tritici* forms 9, 19, 21, 27 and 34 Stak. and Lvne. Their action on differential varieties of *Triticum* spp. is given in a previous publication (17). In the present study Marquis and Kanred, common wheats, Einkorn, and Vernal were used as controls.

The plants studied were inoculated in the usual manner and the rust notes were taken two weeks after inoculation. The results are recorded in table 1. The types of infection are given according to the scale used by Stakman and Levine (17). In this scale 0 designates immunity; 1 and 2, resistance; 3 and 4, susceptibility; X indeterminate reaction.

TABLE 1.—*Reaction of synthetic wild and natural wild emmers to five different physiologic forms of Puccinia graminis tritici*

Physiologic forms of *P. graminis tritici*	Reaction to rust fungus					
	Differential varieties				Wild strains	
	Wheat		Einkorn	Emmer	Synthetic	Natural
	Marquis	Kanred		Vernal		
No. 9	4	0	3	4	4	4
No. 19	2	0	3	0	4	4
No. 21	4	0	1	0	4	4
No. 27	2	0	1	4	4	4
No. 34	4	4	1	0	4	4

As will be seen from the results presented in table 1, the degrees of infection produced by the five physiological forms are quite different on Marquis and Kanred wheats, Vernal emmer, and Einkorn, and yet they all produced a type 4 infection on the two wild emmers. Marquis differentiated forms 9, 21, and 34 from forms 19 and 27. Kanred, being completely susceptible to form 34 and absolutely immune from the other four forms, served as the differentiating host for form 34. Forms 9 and 19 could easily be distinguished from forms 21 and 27 by the difference in the reaction of Einkorn. Vernal served as the differential variety between forms 9 and 27 on one hand, and forms 19, 21, and 34 on the other.

CONCLUSION

The fact that the synthetic wild emmer and the natural wild emmer react alike to different physiologic forms of *P. graminis tritici* furnishes additional proof of their similarity, and supports the view of Love and Craig (12, 13) regarding the probable origin of the natural wild emmer. This experiment also demonstrates again the value of parasitic organisms as physiological reagents in phylogenetic and taxonomic studies.

OFFICE OF CEREAL INVESTIGATIONS,
BUREAU OF PLANT INDUSTRY,
U. S. DEPARTMENT OF AGRICULTURE,
IN COOPERATION WITH AGRICULTURAL EXPERIMENT STATION,
UNIVERSITY OF MINNESOTA.

LITERATURE CITED

1. AAMODT, O. S. The inheritance of growth habit and resistance to stem rust in a cross between two varieties of common wheat. Jour. Agr. Res. **24**: 457–470. 1923.
2. AARONSOHN, A. Agricultural and botanical explorations in Palestine. U. S. Dept. Agr., Bur. Plant Indus. Bul. 180. 1910.
3. CHAPMAN, A. C. Quelques récents progrès de la Chimie analytique. Deuxième partie. Rev. Gén. Sci. **28**: 469–471. 1917.
4. DUFRÉNOY, J. Les réactifs biologiques de l'espèce et la spécificité parasitaire. Rev. Gèn. Sci. **30**: 44–47. 1919.
5. ERIKSSON, J. Ein parasitischer Pilz als Index der inneren Natur eines Pflanzenbastards. Bot. Notizer **1895**: 251–253. 1895.
6. HAYES, H. K., and E. C. STAKMAN. Wheat stem rust from the standpoint of plant breeding. Proc. Ann. Meeting West. Canad. Soc. Agron. (1921) **2**: 22–35. 1922.
7. ————, and O. S. AAMODT. A study of rust resistance in a cross between Marquis and Kota wheats. Jour. Agr. Res. **24**: 997–1012. 1923.
8. JOHNSTON, C. O., and C. W. BOWER. A method of detecting mixtures in Kanred wheat seed. Jour. Amer. Soc. Agron. **16**: 467–470. 1924.
9. KLEBAHN, H. Die wirtswechselnden Rostpilze. Versuch einer Gesamtdarstellung ihrer biologischen Verhältnisse. 447 p. Berlin. 1904.
10. LEGRAND, L. Les caractéristiques bio-chemiques de l'espèce. Rev. Gén. Sci. **29**: 333–340. 1918.
11. LEVINE, M. N., and E. C. STAKMAN. A third biologic form of *Puccinia graminis* on wheat. (Preliminary paper.) Jour. Agr. Res. **13**: 651–654. 1918.
12. LOVE, H. H., and W. T. CRAIG. The synthetic production of wild wheat forms. Jour. Heredity **10**: 51–64. 1919.
13. ————, ————. The genetic relation between *Triticum dicoccum dicoccoides* and a similar morphological type produced synthetically. Jour. Agr. Res. **28**: 515–520. 1924.
14. PUTTICK, G. F. The reaction of the F_2 generation of a cross between a common and a durum wheat to two biologic forms of *Puccinia graminis*. Phytopath. **11**: 205–213. 1921.
15. STAKMAN, E. C., and F. J. PIEMEISEL. A new strain of *Puccinia graminis*. (Abstract.) Phytopath. **7**: 73. 1917.

16. ————————, M. N. LEVINE, and J. G. LEACH. New biologic forms of *Puccinia graminis*. (Preliminary paper.) Jour. Agr. Res. **16**: 103–105. 1919.

17. ————————, and M. N. LEVINE. The determination of biologic forms of *Puccinia graminis* on *Triticum* spp. Minn. Agr. Exp. Sta. Tech. Bul. 8. 1922.

18. VAVILOV, N. I. (WAWILOW, N.). Beiträge zur Frage über die verschiedene Widerstandsfähigkeit der Getreide gegen parasitische Pilze. Trudy Selek. Stan. Moskov. Selskokhoz Inst. **1**: 1–108. (In Russian, German résumé, p. 90–108.) 1913.

19. ————————. Immunity to fungous diseases as a physiological test in genetics and systematics, exemplified in cereals. Jour. Genetics **4**: 49–65. 1914.

20. ————————. Immunity of plants to infectious diseases. Izv. Petrovsk. Selskokhoz. Akad. **1918**: 1–239. (In Russian, English résumé, p. 221–239.) 1919.

ROOT KNOT ON SUGAR CANE IN PORTO RICO

JULIUS MATZ

WITH TWO FIGURES IN THE TEXT

Since the middle of the summer of 1924 the writer has been finding nematode-infected root swellings or "root knot" of sugar cane in widely separated areas in southern Porto Rico. The exact extent and severity of this infestation is not yet determined, but it has undoubtedly caused the lack of growth in older cane as well as the death of young cane in a number of fields in several concentrated areas.

This nematode infection of cane can be detected by two distinct symptoms: first, by a deep, waxy, or golden yellow instead of the normal green coloration in the leaves of the older plants. This yellowing, which often occurs in rather indefinite wide bands, usually starts from the tips of the leaves and spreads downward to their sheaths. This color is distinct from the pale or white-yellow rather narrow bands in chlorotic leaves. Second, in young cane three or four months old the outermost leaves become shriveled and streaked longitudinally with red or copper colored areas divided by long, dry strips, and the whole plant becomes stunted and takes on a bunched or small-broom like appearance. Cane plants showing these symptoms when pulled up were found to have in the newer portions of their roots, mostly at the root tips, visible swellings or galls of about twice the original diameter of the root (Fig. 1). These swellings were enlargements of the outer fleshy layers only, while the central woody parts were not deformed. Nematodes are embedded in these swellings. In the older, less conspicuous galls which occur throughout the length of the roots are found the impregnated female nematodes. These females are about 1 mm. in length, milky white, glistening, usually in the form of a diminutive bulb with the extended thin neck and head distinguishable from the rest of the egg-full body (Fig. 2, a). As the outer fleshy layer of the cane roots ultimately shrinks and becomes spongy and brown, the galls become greatly reduced. In this condition by bending the root and thus breaking the epidermis, the larger females are exposed and found situated in rounded cavities. These cavities become larger after the disappearance of the inhabiting nematodes, owing to the shrinking of the surrounding spongy tissues (Fig. 2, b).

The main apparent physical injury which this nematode causes is the small cavities in root tips which are finally destroyed. A general decay of the roots does not usually occur, although they may become riddled with

FIG. 1. "Root Knot" on sugar cane roots. ×2.

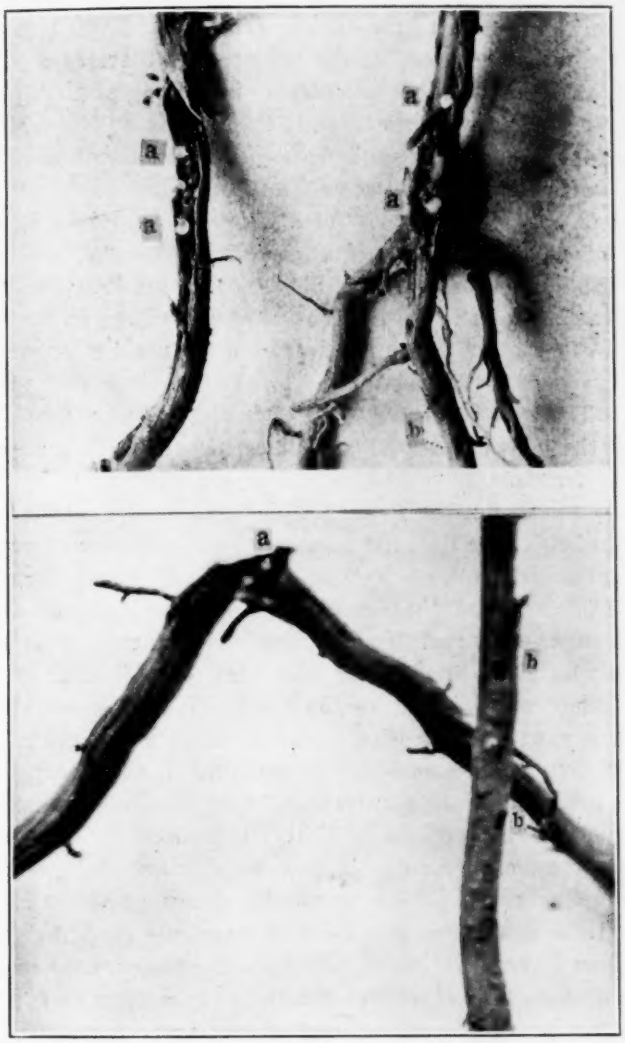

FIG. 2. Sugar cane roots infected with nematodes. *a*, the white globular but pointed females full of eggs are exposed after tearing away the epidermis of the root; *b*, empty old nematode cavities in roots. ×3.

holes, but root-tip decay was quite commonly seen in association with nematode infestation. Sometimes, however, many new rootlets grow out from near a gall, but the newer roots in turn may also become infested. The effect on the growth of the cane is very marked when nematodes are abundant. The cane leaves become yellow, and there is a very evident retardation of growth of the whole plant. The death of young cane due to severe nematode injury has been seen in three fields.

Nematode infestations of sugar cane have been found only in loose or sandy soil, or in land with a loose or sandy subsoil.

Krüger (2) says that Prins, Treub, Saltwedel, and he have observed two types of nematodes, *Tylenchus sacchari* Saltwedel, and *Heterodera radicicola* Müller, on sugar-cane roots in Java, between the years 1885–1887. Tylenchus apparently did not produce swellings in the roots, while Heterodera, quoting Dr. Krüger, "builds on the roots of sugar cane up to hazel-nut size galls" (Translation). Neither of these two species would coincide with the rather small gall-producing nematode in Porto Rico. Because of the gall-forming habit of this nematode, it is also placed in the genus *Heterodera*.

Cobb (1) relates how he found a Tylenchus on the roots of sugar cane in Hawaii in 1907. He does not mention the appearance of galls or swellings in the attacked roots.

Rands (3) described the damage caused by pitting of the terminal portion of sugar-cane roots in Louisiana by a small snail (*Zonitoides arboreus* Say). These cavities or pits were 0.3–2.0 mm. in depth and diameter. They were similar to the cavities made by nematodes in the roots of sugar cane in Porto Rico, where no snails were associated with the pitted roots, but where nematodes were found in the unexposed cavities. Rands does not mention the occurrence of swellings or galls associated with snail injury.

The symptoms of nematode injury are distinct and peculiar to this affection of cane roots. While a partial decay of the roots is caused directly by these nematodes, root knot becomes only an added phenomenon to, rather than an explanation of, root diseases of sugar cane in Porto Rico. Other root diseases have their own distinctive symptoms and causes, as has been shown in previous publications. Apart from nematode injury and root infection by *Plasmodiophora vascularum* Matz there is no clearly defined cane-root disease on the irrigated south coast lands of Porto Rico.

This root knot on sugar cane occurs on loose, though sometimes wet, more or less sandy soils on varieties, Cristalina, BH 10 (12), and SC 12/4. It has not been seen on the heavier, moisture-retaining silt or clay soils. According to the observation of the Javanese investigators, however, mois-

ture seems to favor nematode occurrence on sugar cane in Java. While on high land, after a prolonged dry period, living nematodes were rather rare there.

The bad effects of the nematodes were overcome in one field of young cane growing on a porous soil consisting of about an 8-inch top black layer underlaid with several feet of brown sand and coarse gravel by applying a layer of barnyard manure to the roots of the cane and then covering this with soil, after which the field was kept moist by frequent irrigation. This gave the cane plants an opportunity to develop a new root system in a new and fertile layer of soil. This seems to be a plausible means of control as the nematodes seem to be most abundant and are at least more injurious in soils where there is less stimulus to root growth.

FORTUNA,
PORTO RICO.

LITERATURE CITED

(1) COBB, N. A. *Tylenchus similis*, the cause of a root disease of sugar cane and banana. Jour. Agr. Res. **4**: 561–568. 1915.
(2) KRUGER, W. Das Zuckerrohr und seine Kultur. Magdeburg and Wien. 1899.
(3) RANDS, R. D. Snails as predisposing agents of sugar-cane "root disease" in Louisiana. Jour. Agr. Res. **28**: 969–970. 1924.

OAT BLAST

CHARLOTTE ELLIOTT

In oats throughout the United States there is present each year a condition of some of the spikelets which in this country has been designated as "blast" or "sterility" and in England as "blindness," "deafness," or "white ear." These blasted or undeveloped spikelets usually are white and range from minute rudiments to fairly well developed empty glumes. Occasionally the larger empty glumes contain chlorophyll. The numbers of blasted spikelets in different fields, and under different environmental conditions, vary considerably. At a conservative estimate they may in some cases amount to 40 per cent of the total number. In North America this condition of the spikelets has been attributed to thrips (2) and to the bacterial disease known as "halo blight" (3). In England frit flies were found associated with the blasted spikelets and considered as the cause (4).

The results of observations and experiments in Wisconsin during 1918 and 1920 (1) showed conclusively that, while the bacterial disease known as halo blight is in some cases associated with blast, on the whole there is no connection between the two; blasted spikelets appearing quite independently and in fields where the bacterial disease does not occur. The results of this work also indicate that environmental conditions may be important factors in the production of blast. To determine the possibility of a correlation between temperature and rainfall at heading time on the one hand and blast on the other and to learn whether or not there are rather constant varietal differences in blast from year to year, counts have been made for the past three years on a number of varieties of winter oats grown in the varietal experiments conducted by the Office of Cereal Investigations at Arlington Farm, near Rosslyn, Va., under the direction of T. R. Stanton and J. W. Taylor. All spikelets were counted as blasted in which no kernel developed. The results of this preliminary work are summarized in table 1.

The varieties listed in the tables were grown in fortieth-acre plats. On 24 panicles selected at random in each plat counts were made of the number of normal and blasted spikelets. For most of the varieties the plats were replicated several times, hence the counts were correspondingly repeated. Thus the number of panicles counted amounted to from 2 to 4 times the twenty-four for each plat. Averages of the entire number in each variety were taken and percentages of blast determined.

TABLE 1—*Average percentages of blast in winter oat varieties grown at Arlington Farm, Virginia, in 1922–24*

1922			1923			1924		
Variety	C. I.[a] No.	Pct. blast	Variety	C. I. No.	Pct. blast	Variety	Pct. blast	C. I. No.
Hatchett	838	6.38	Hutcheson Selection	947	17.77	Fulghum	708	11.54
Kanota	839	6.84	Fulghum	708	19.57	Kanota	839	15.61
Fulghum	708	8.98	Kanota	839	21.79	Hatchett	838	21.64
(Black)[b]	691	13.47	(Black)[b]	691	25.45	(Black)[b]	691	22.08
Hutcheson Selection	947	15.67	Winter Turf	541–4	26.13	Hutcheson Selection	947	25.58
Culberson	273	16.16	Red Rustproof	1815	31.05	Aurora	831	27.54
Dwarf Culberson	748	17.43	Culberson	273	32.79	Culberson	273	27.92
Aurora	831	20.61	Winter Turf	435–4	33.39	Dwarf Culberson	748	28.66
Winter Turf	541–4	22.05	Winter Turf	431	34.21	Bicknell	206–155	29.22
Red Rustproof	1815	23.93	Bicknell	206–155	34.51	Winter Turf	541–4	30.29
Winter Turf	435–4	24.84	Dwarf Culberson	748	34.95	Red Rustproof	1815	31.52
Winter Turf	431	26.52	Lee	2142	37.00	Winter Turf	431	32.53
Bicknell	206–155	27.65	Aurora	831	37.48	Winter Turf	435–4	32.64
Ferguson Navarro	966	28.00	Custis	2141	40.49	Lee	2142	38.23
			Ferguson Navarro	966	46.62	Custis	2141	38.47
						Ferguson Navarro	966	45.47

[a] Cereal Investigations accession number.

[b] An unnamed black strain similar to Hutcheson Selection.

The varieties are arranged in the order of increasing percentages of blasted spikelets. A comparison of the data available for the three years brings out three facts which throw some light on the problem of blast in oats.

First. Varietal differences in the amount of blast appear to be fairly constant from season to season. The five varieties, Hatchett, Kanota, Fulghum, Hutcheson Sel., and (Black) C. I. No. 691, show the lowest percentages throughout the three years. Culberson and Dwarf Culberson are intermediate, and Ferguson Navarro, Lee, and Custis consistently show high percentages of blast. The greater variability of some of the varieties may or may not be due to the limited data.

Second. Percentages of blast in all varieties vary from year to year, all percentages being higher in some seasons and consistently lower in others. In 1922, all of the varieties listed showed comparatively low percentages of blast. In 1923 the percentages throughout the list are much higher—in some varieties more than double those of the previous year. In 1924 the percentages are intermediate with the exception of 4 varieties, Hutcheson, Red Rustproof, Winter Turf 541–4, and Lee. The decided contrast in percentages of blast in 1922 and 1923 seem to indicate that certain seasons are much more favorable for the development of blast than other seasons, and that environmental conditions are possible factors in bringing about these differences. As the oats were grown on the same farm and on practically the same type of soil throughout, this factor may for the present be eliminated. In attempting to correlate the high percentages of blast with rainfall and temperature at the time of heading, the following figures are of interest. The ranges in the percentages of blast for the three years are respectively: 6–28%, 17–46%, 11–45%. The total precipitation for May of each year, the month when the plants head out, was 4.53 inches, 1.49 inches, and 6.59 inches respectively. It is at once evident that in 1923, when percentages of blast were highest, the rainfall at heading time, instead of being above normal was much lower than in either 1922 or 1924 and considerably below the normal of 3.83 inches. Furthermore the exact precipitation dates in 1923 do not coincide with dates of heading of the different varieties. In 1923 all varieties, with the exception of Winter Turf, headed during a period of no rainfall. In 1924 most of the varieties headed at a time when there was some rainfall nearly every day. Weather reports for 1922 and 1923 show that the blast of 1923 is not connected with drought conditions during earlier months, for precipitation was near or above normal in the preceding months. Variations in temperature were greater in May, 1923 and 1924, than in 1922; but for the present no attempt is made to connect these

wider ranges in temperature with the greater number of blasted spikelets.

Third. The varieties which show the highest percentages of blast, i.e., Ferguson Navarro, Custis, and Lee, are either of known or suspected hybrid origin. Lee and Custis are new varieties developed from a hybrid of Aurora × Winter Turf by T. R. Stanton. According to Mr. Stanton there is some reason for thinking that Ferguson Navarro also is of hybrid origin as it shows some characteristics of both red and common oat varieties. It originated as a stray plant in a field of Red Rustproof oats in Navarro County, Texas.

What is known regarding the sterility which follows certain crosses both in plants and animals may have some bearing on the high percentages of undeveloped spikelets in the hybrid varieties Lee and Custis and also in Ferguson Navarro.

Work along similar lines is in progress.

LABORATORY OF PLANT PATHOLOGY AND OFFICE OF CEREAL INVESTIGATIONS,
BUREAU OF PLANT INDUSTRY, U. S. DEPARTMENT OF AGRICULTURE,
WASHINGTON, D. C.

LITERATURE CITED

1. ELLIOTT, CHARLOTTE. Sterility of oats. U. S. Dept. Agr. Bul. 1058: 1–8. 1922.
2. HEWITT, C. G. Sterility in oats caused by thrips. Jour. Econ. Ent. 7: 211–218. 1914.
3. MANNS, T. F. The blade blight of oats, a bacterial disease. Ohio Agr. Exp. Sta. Bul. 210: 91–167. 1909.
4. ROEBUCK, A. Frit fly (*Oscinis frit.*) in relation to blindness in oats. Ann. Appl. Biol. 7: 178–182. 1920.

PHYTOPATHOLOGICAL NOTES

Polyporus schweinitzii Fr. on Douglas Fir in the Eastern United States.—Very severe losses from cankers attributed to *Phomopsis pseudotsugae* Wilson have been reported in Scotland in plantations of Douglas fir, *Pseudotsuga taxifolia* (Lam.) Britt. Since trees of this species had been shipped to the United States among the many importations of conifers from Great Britain before the present quarantine laws went into effect, it is feared that this disease may have been introduced in this manner. The Office of Investigations in Forest Pathology, as opportunity offers, is examining all plantations of Douglas fir for this disease.

One of the small plantations of this species inspected August 19, 1924, is located on the Vanderbilt estate near Biltmore, North Carolina. The trees of Douglas fir in this particular area were four-year-old transplants when set out in 1896 by Dr. C. A. Schenck. The *Phomopsis* canker was not found at the time of inspection but it was noted that the red-brown butt and root-rot due to *Polyporus schweinitzii* Fr. was present and causing considerable damage. Six trees were found wind-thrown in a slight depression on a northwestern slope, despite a cover of planted white pine surrounding the plantation. The fallen trees ranged from 18 to 24 feet in height and from 3½ to 5 inches D. B. H. The butts and roots, especially the main tap roots, were badly rotted and greatly weakened by *Polyporus schweinitzii*. At the base of each of two of the wind-thrown trees which were still alive, typical sporophores of this fungus were found in direct association with the red-brown rot, indicating that it was the cause of the decay.

This plantation of Douglas fir has not thrived. Although it has not been thinned or given much care, and some of the trees have apparently been cut for Christmas greens, the primary cause of failure is very probably the attack of *Polyporus schweinitzii*. This fungus has never been reported seriously injuring young Douglas fir trees in the northwestern United States, although it is very destructive to older ones there. This indicates either a greater virulence in the strain of the fungus present or a greater susceptibility of the host tree in the locality near Biltmore.

Polyporus schweinitzii is known to attack various species of pine, spruce, fir, and hemlock in the eastern United States, and in this instance the fungus probably spread from trees of some of these species to those of the Douglas fir. This fungus has been reported as attacking young Douglas fir in Great Britain, and is frequently found in other conifers in Europe. It

is possible that introduced species by a change of habitat may be rendered more susceptible to root rots than trees in the native stands.—G. G. HEDGCOCK, G. F. GRAVATT, AND R. P. MARSHALL, OFFICE OF INVESTIGATIONS IN FOREST PATHOLOGY, BUREAU OF PLANT INDUSTRY, WASHINGTON, D. C.

Fire at Clemson College. The Agricultural Hall at Clemson College burned early in April. The Division of Botany and Bacteriology was on the first floor and suffered heavy losses. The following members of the personnel of the Division lost their files of reprints and would appreciate receiving complete sets of separates: D. B. Rosenkrans, pathology, physiology, and forestry; Mr. and Mrs. W. B. Aull, bacteriology and general botany; W. D. Moore, pathology (reprints received more than a year ago were saved); L. M. Fenner, pathology; and C. A. Ludwig, pathology and physiology. The Experiment Station library also was destroyed, and the librarian, Mrs. Crown Torrence, would be pleased to receive separates and bulletins.—C. A. LUDWIG, CLEMSON COLLEGE, SOUTH CAROLINA.

BOOK REVIEWS

MANUAL OF VEGETABLE-GARDEN DISEASES. By C. C. Chupp, Ph.D. New York. The Macmillan Co., 1925, pp. 647, figs. 155. Price, $4.00.

In 1874 Sorauer's classic work entitled, "Handbuch der Pflanzenkrankheiten," was published. Twenty-two and twenty-three years later, "Pilzpärasitaren Krankheiten der Pflanzen," and "Diseases of Plants Induced by Cryptogamic Parasites," by Frank and by von Tubeuf and Smith, respectively, made their appearance. These efforts, while good in the light of the knowledge of plant diseases at that time, were soon out-of-date. Some years after the appearance of the works by Sorauer, Frank, and von Tubeuf, Americans entered the field. As an outgrowth of the development of the science in the United States, a number of books, texts as well as handbooks of reference, attempting to cover the diseases of crops as a whole or in part, have appeared. Most of these books have not quite come up to anticipation either from the standpoint of a reference for research workers or from the standpoint of those uninitiated into the realm of phytopathology. Chupp, with a book of 647 pages, entitled "Manual of Vegetable-Garden Diseases," is the last to enter the field. The purpose of the book as implied in the language of the author is to bring "together all the material in such a form that it is available to the plant pathologists generally and to the growers and extension specialists in particular." To bring together *all* the material in an available form is no small undertaking. No regional territorial limitations are claimed for the book, from which it will be inferred to be of world-wide application.

The book is attractively bound, printed with a clear type on good paper, and presents an attractive appearance. The entire subject-matter is divided into twenty chapters. Each of the first eighteen chapters treats of the specific diseases of a crop or group of crops generally related. The nineteenth chapter discusses the various phases of soil sterilization, and the twentieth treats of the use and application of fungicides. An entire chapter is given to the diseases of the more important crops or to the crops whose diseases are best known. This mode of procedure, however, is not always followed, since chapter three is given to the diseases of beets, carrots, and chicory; chapter eleven to okra, parsley, and parsnip; and chapter fifteen to rhubarb and salsify. These combinations are apparently made wholly on the grounds of their alphabetical order, notwithstanding the fact that a better combination could have been made on the basis of common diseases, as, for example, chicory and lettuce. As a matter of fact, it would probably have been better, both from the standpoint of consistency and clearness, to have given an entire chapter to each crop, even though it is a relatively unimportant one and the diseases few.

Each disease, if an important one, is discussed under symptoms, cause, and control. This arrangement of subject-matter is good and is helpful to the reader in finding the particular features of the disease in which he is interested.

There are 155 illustrations reproduced as text figures. Many of these illustrations are typical of the disease as a whole and are well reproduced. Others, on the other hand, are not typical or are poorly reproduced. It is to be regretted that the author copied so many of the illustrations from bulletins and journal articles. In many cases copies were made when high-grade prints or even negatives could have been secured or borrowed.

The author shows a lack of familiarity with the diseases of southern crops. One looks in vain for any mention of cassava, chayote, yam, udo, and dasheen, all of which are grown in the United States and some of which are becoming important food crops. If, as claimed by the author, the book is to be of particular use to the extension specialist, it would be highly desirable to have information on the diseases of these crops, if any such occur, made available for him in a manual of this sort. Furthermore, if diseases of certain vegetable crops are unknown or have not been studied, the extension specialist would welcome such information.

The author has discussed in more detail than would appear necessary the well-known diseases of the major crops. One hundred and fifteen pages are devoted to the potato alone, thirteen pages to a discussion of *Rhizoctonia*, and eight to late blight. These diseases, as well as potato scab, are well known, even to the majority of farmers where they occur. It would seem that a briefer discussion of such dseases would have sufficed, thus giving space for the inclusion of crops that have been omitted.

As a substitution for the omissions mentioned above, one finds included a discussion of some, but not all diseases, which have been reported only in foreign countries, as, for example, Zopfia root-canker of asparagus, caused by *Zopfia rhizophila*. Leptothyrium canker of asparagus caused by *Leptothyrium asparagi*, Phoma root-rot of carrot caused by *Phoma sanguinolenta*, Corynespora leafspot of cucurbits caused by *Corynespora melonis*, Phytophthora fruit-spot of eggplant caused by *Phytophthora melongenae*, and black dot-rot of eggplant caused by *Rhabdospora melongenae*.

Some diseases of important crops in the United States have not been mentioned, as, for example, *Rhizoctonia* and root-knot of sweet potatoes, damping-off of eggplant caused by *Pythium*, and hollow stem of tomatoes. Some of these diseases are of more economic importance and more destructive than some of those mentioned.

The book for a first edition is relatively free from typographical errors and misstatements. A few have been noted. On page 38, line 8, we find "ascerigerous"; on p. 38, line 11, "chalamydospores"; on p. 43, line 13,

"open sori or short stalks"; on p. 630, line 1, "perthecium"; on p. 58, line 34, "yars" for "years," and on p. 379, line 36, "Weimar" for "Weimer."

Each chapter is closed by the citations of literature. This is a commendable feature of the book. The literature cited has for the most part been carefully selected from the more reliable sources and from the more recent publications. This is particularly noteworthy, since the method of handling citations will facilitate acquaintance with original or more detailed treatment of subjects involved.

Some unfortunate mistakes have been made in the citing of references. For example, on p. 524, line 2, we find "Phytopath." which should read, "Jour. Agr. Research." On p. 398, line 36, "The regeneration of first generation hybrid potatoes to the wart disease" should read "The reaction of first generation hybrid potatoes to the wart disease"; and on p. 536, line 3, "Effect of copper soap spray mixtures on control of tomato leaf-spot" should read "Effect of copper soap and of bordeaux soap spray mixtures on control of tomato leaf spot."

The book is undoubtedly the best that has yet been produced in this particular field. In that there is brought together for ready reference information relative to the identification and control of the more common vegetable diseases, the book is one which will be useful to extension workers as well as to the investigator. From the standpoint of the research worker at least, the author often speaks with more positiveness and finality than the facts in the case will warrant; likewise, deductions are sometimes made which from the information contained in the literature hardly seem justified.

All in all, Dr. Chupp is to be commended for having acquitted himself so well at such a difficult task. He has not only demonstrated a first-hand knowledge and familiarity with many of the garden crop diseases, but he has combined this information with that contained in a mass of literature to produce a book which is not only better than any book of its kind yet published but which is really good. It is to be hoped that the book will receive a careful re-editing before another edition is printed.

L. L. HARTER

OFFICE OF COTTON, TRUCK, AND FORAGE
CROP DISEASE INVESTIGATIONS,
U. S. DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.